A COMPARATIVE STUDY OF THE SEED BANK DYNAMICS OF TWO CONGENERIC ALIEN INVASIVE SPECIES

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STATEMENT OF CONTRIBUTIONS BY CO-AUTHORS OF PAPERS

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Mr I.A.W. Macdonald assisted with the early planning of the fieldwork and preparation of the manuscript. Prof. J. Juritz assisted with statistical analyses.

Paper 4 (Jeffery, Holmes & Rebelo)

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Paper 5 (Holmes, Dennill & Moll)

Ideas behind this paper were discussed jointly amongst the three authors. Dr G.B. Dennill contributed seed viability data and I provided seed bank data.

Paper 6 (Holmes & Rebelo)

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Except where specified above, I testify that this thesis is entirely my own work.

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Abstract

The unique vegetation in the lowlands of the fynbos biome is threatened by alien *Acacia* encroachment. The seed bank dynamics of the two most widespread invaders in the region, *Acacia saligna* and *A. cyclops*, was studied to elucidate those factors contributing most to their invasive success. This information was then used to assist in developing optimal control methods. On the basis of information available prior to this study, it was predicted that both species would have large, persistent seed banks in the soil, and that seed bank processes would provide the key to invasive success: namely, high seed longevity and heat-stimulated germination.

Seed banks were monitored for several years following clearing of the parent stand, using either sites sampled in an earlier study, or sites providing chronosequences of clearing dates. Concurrently, a demographic study of the species' seed banks, including processes from seed rain through to seedling emergence and survival, was done in dense *Acacia* stands and in fynbos vegetation.

Acacia saligna seed banks conformed to predictions, being large and persistent owing to high percentage viability and water-impermeable dormancy. Seed banks accumulate rapidly under dense stands and are "disturbance-coupled" as they have potentially high longevity unless stimulated to germinate by fire. Although *A. cyclops* seed banks also may be large and long-lived, they display variable percentage viability and dormancy, with the majority of a seed cohort surviving less than a year. *Acacia cyclops* seed banks do not respond to heat treatment and appear to be "disturbance-uncoupled".

Thus, contrary to prediction, different seed bank processes provide the key to invasive success in the two species, despite their taxonomic link and invasion into similar fynbos communities. In *A. saligna* key processes are high seed longevity and a rapid, positive germination response to fire. Key processes in *A. cyclops* would appear to be those which characterize the species as an opportunist: avian

dispersal into new areas and the ability to germinate in the absence of disturbance-related cues. However, the maintenance of a small persistent seed bank reduces the risk of local extinction and also may have contributed to its invasive success.

An indigenous seed-sucking insect (*Zulubius acaciaphagus*; Hemiptera, Alydidae) has successfully colonized *A. cyclops* in South Africa, whereas no equivalent pre-dispersal seed predator has been observed to attack *A. saligna*. Feeding by *Z. acaciaphagus* reduces seed viability and increases seed rotting. In areas where the insect attains a high population density it may reduce the rate of seed accumulation in the soil.

Acacia seeds on the ground are removed by indigenous ants and rodents. In general removal is rapid and complete in light infestations, whereas it may be slow and incomplete in dense stands. As resident granivores have the potential to consume the entire seed crop in light infestations, it is suggested that ants have played a critical role in burying and thus accumulating *Acacia* seeds in the soil.

Seed burial is facilitated by the actions of burrowing animals and in sandy soils seeds are commonly distributed to a depth of 300 mm. Seeds may produce a viable seedling only from depths of 150 mm and above, however. Despite initially high levels of dormancy and viability, in both species a large proportion of seeds buried in the soil may be lost in the first year. Seed longevity in *A. saligna* is much higher than in *A. cyclops*, but in both species it declines with depth of burial. Decay rates are significantly lower in the second than in the first year and seeds appear to follow a "Deevey Type III" survivorship curve, rather than the log-linear or "Deevey Type II" curve, which has been postulated for soil-stored seeds.

Clearing stands by burning results in significant seed bank reductions in both species and is superior to non-burning methods in *A. saligna*. However, in *A. cyclops*, felling alone results in a significant decrease in seed banks and burning methods may be superior only at sites where the seed bank is concentrated near to the soil surface. The potentially high seed longevity, even in a small proportion of

the seeds produced in the case of *A. cyclops*, emphasizes the importance of follow-up control in any clearing programme.

It is recommended that future research should quantify seed removal by avian dispersers, especially in *A. cyclops*, as this may indicate the necessity of introducing seed-attacking agents in the control of the invaders. Other fields meriting further study are colonization of *A. cyclops* by the indigenous alydid bug, *Zulubius acaciaphagus*, and dispersal of *Acacia* seeds by indigenous ants.

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Preamble

The international SCOPE (Scientific Committee on Problems of the Environment) project on the ecology of biological invasions had its origins amongst mediterranean terrestrial ecosystem ecologists, being first proposed at an international workshop on mediterranean ecosystems in 1980. The South African Programme was designed to contribute directly to the international project, with three broad questions being posed (Ferrar & Kruger 1983):

(1) What are the factors that determine whether a species will become an invader or not?

(2) What are the site properties that determine whether an ecological system is susceptible or resistant to invasion?

(3) How should management systems be developed, using the knowledge gained from answering (1) and (2) ?

Through question (3) the programme was intended to relate primarily to nature conservation problems.

At a workshop on invasive alien organisms of the fynbos biome (Macdonald & Jarman 1984), the extreme importance of the alien *Acacia* species as invaders in the region was highlighted. The research priority receiving the second highest rating by participating scientists and managers was "A study of the dynamics of soil-stored seed of alien *Acacia* species following a variety of clearing procedures".

In response to this identified research gap, a three-year project entitled "Dynamics of alien *Acacia saligna* and *Acacia cyclops* seed banks following different clearing procedures in the SW and southern Cape" was approved and funded by the Ecosystems Programmes (Nature Conservation Section) of the C.S.I.R.. Three main objectives were identified:

(1) To quantify short-term and long-term changes in seed density following different clearing procedures.

(2) To investigate the fate of seed on and in the soil.

(3) To investigate the potential of buried seed to produce new plants.

The ensuing thesis is based on research findings from this project (Holmes *et al*. 1987).

I INTRODUCTION

(a) **Rationale**

The fynbos biome, which is famous for the richness and diversity of its flora (Bond & Goldblatt 1984), is threatened by invasions of alien plants, particularly trees and shrubs (Kruger 1981, Macdonald 1984). Control of alien woody plants is currently the most expensive aspect of vegetation management in the biome (Macdonald *et al.* 1985).

In lowland ecosystems, the Australian acacias *Acacia saligna* (Labill) Wendl. and *A. cyclops* A. Cunn. ex G. Don are the most widespread invaders (Macdonald & Richardson 1986). They typically form dense thickets, suppressing the indigenous vegetation and thus reducing the species richness of the community (Roux & Middlemiss 1963, Taylor 1983). The alien acacias accumulate large, putatively long-lived seed banks in the soil, which are thought to be a major factor contributing to their success in South Africa (Dean *et al.* 1986) and to the difficulty experienced in their control (Milton & Hall 1981).

A comparative study of two congeneric alien species may reveal important similarities or differences in life-history characteristics leading to invasive success, and thus may promote the formulation of general hypotheses on invasive potential and assist in the development of more effective control techniques (cf. Mooney & Drake 1987).

(b) **Description and ecology of study plants**

In common with other alien species, *Acacia saligna* and *A. cyclops* have been studied more in their country of introduction than in their country of origin. However, some recent publications on *A. cyclops* (e.g. Gill 1985, Fox 1985, O'Dowd & Gill 1986) have provided an Australian perspective on this species.

Both species are evergreen shrubs or small trees. *Acacia saligna* has a willowy appearance and may attain a height of nine metres, whereas *A. cyclops* is

typically a dense low-branching shrub, which sometimes may attain a height of six metres (Stirton 1978). Both species bear phyllodes in place of true leaves. Two-year-old saplings may set seed, but maximum seed production is not reached until at least five years of age (Milton & Hall 1981).

Acacia saligna flowers in early spring, and pods ripen and dehisce in early summer, releasing seeds onto the ground, and falling soon afterwards (Stirton 1978). Seed rain in South Africa is in the order of 5 000 seeds.m^{-2} p.a. under mature trees (Milton & Hall 1981). The dispersal unit is a hard black seed (about 16 mg fresh mass) which bears a small, hard, white elaiosome, attractive to ants (O'Dowd & Gill 1986).

Acacia cyclops mostly flowers between October and May, with a peak in early summer (Stirton 1978). Pods ripen after one year, then dehisce to display the conspicuous dispersal units. The latter are composed of hard, dark brown to black seeds (about 33 mg fresh mass), each encircled by a large red aril. This colour combination attracts birds for dispersal (Glyphis *et al.* 1981, O'Dowd & Gill 1986, Forde 1986). The retention of seeds and pods on the tree (Glyphis *et al.* 1981) and a long (five month) fruit season (Knight 1986) further promotes avian dispersal. Seed rain in South Africa is in the order of 1 000 seeds.m^{-2} p.a. under mature trees (Milton & Hall 1981).

Both species are native to mediterranean-climate regions of Australia, *A. saligna* occurring in SW Western Australia and *A. cyclops* extending from SW Western Australia into South Australia (Maslin & Pedley 1982). *Acacia saligna* occurs principally in dry sclerophyll forest and temperate woodland, although it also extends into low semi-arid woodlands, and mallee and heath communities (Hall & Turnbull 1976). It grows on a wide range of soil types from nutrient poor and calcareous sands to moderately heavy clays and podzolics (Hall & Turnbull *ibid.*). *Acacia cyclops* has a wholly coastal distribution and occurs principally in coastal heath and scrub communities (Fox 1985). It grows on calcareous and sandy soils and is a calcicole (Fox *ibid.*).

In its native habitats *A. saligna* is subject to periodic disturbance through fire (Christensen *et al.* 1981), whereas *A. cyclops*, which is rarely subject to fire, may be disturbed by natural erosion-sediment cycles in coastal areas (Gill 1985).

In summarizing the ecology of the species it is useful to consider those features, or 'vital attributes', which relate to their persistence during a disturbance and to their subsequent arrival, establishment and growth (Noble & Slatyer 1980), as these attributes are likely to be important in their establishment and spread in alien lands. Based on research completed prior to this study (mostly in South Africa), *A. saligna* maintains a reserve of dormant seeds in the soil (Milton & Hall 1981) in addition to resprouting from damaged trunks (Macdonald et al. 1985), which yields vital attribute 'S' (for long-lived seed-store), since the combination of these two patterns of availability is still equivalent to that of the seed-store alone (Noble & Slatyer 1980). *Acacia cyclops* is also thought to accumulate dormant seeds in the soil and, in addition, has long-distance seed dispersal (Milton & Hall 1981). This combination is considered to be equivalent to vital attribute 'D' (for seed dispersal) (Noble & Slatyer 1980). Both species may establish and grow at a site immediately following a disturbance, but do not continue to recruit individuals in closed stands (pers. obs), resulting in relatively uniform-aged cohorts. In relation to other dominant species present in fynbos communities, the acacias take a short time to reach reproductive maturity after a disturbance (two years), have a fairly long life-span (at least 25 years, pers. obs) and are unlikely to become locally extinct, owing to seed reserves in the soil, resprouting capabilities in *A. saligna* and dispersal of *A. cyclops* propagules into the area by birds. In theory, *A. cyclops* displays the vital attribute 'D' which enables it to invade new habitats, whereas *A. saligna* cannot do so without the assistance of people. Once present in an area, however, the early onset of reproduction, together with high seed production and the accumulation of seeds in the soil, provides the acacias with potential for local spread and density increase following subsequent disturbances.

(c) **Invasive history**

The earliest known introductions to the SW Cape occurred in 1848 (*A. saligna*) and 1857 (*A. cyclops*) (Shaughnessy 1980). The species were planted for a variety of reasons, notably drift sand control, but also for afforestation, hedges, nurse plants, erosion control, and in *A. saligna*, tanning bark (Shaughnessy *ibid.*). The species continued to be planted during the latter half of the nineteenth century, and despite a growing antagonism towards exotics amongst botanists at the turn of the century, which culminated in a warning of the dangers of alien plants in the Wicht Report (1945), they continued to be planted until as recently as 1951 (Shaughnessy *ibid.*). Control operations in alien-infested areas of the lowlands began sporadically in the 1940's (Macdonald *et al.* 1985), but despite these early attempts, *A. saligna* and *A. cyclops* currently infest large areas of strandveld, coastal fynbos, renosterveld, and *A. saligna* occasionally in mountain fynbos, vegetation types (Macdonald & Jarman 1984).

A knowledge of historical ecology is crucial to the interpretation of alien invasions (Shaughnesy 1980, Mack 1985): the currently widespread distribution of *A. saligna* and *A. cyclops* may largely reflect the original human dispersal of those species, and furthermore their establishment and spread was often promoted by major disturbance or even removal of the vegetation cover (Shaughnessy 1980). Cultivation appears to facilitate alien *Acacia* encroachment (Brownlie 1982).

That *A. saligna* and *A. cyclops* have persisted in South Africa, and have formed dense stands and spread into previously uninfested areas (Taylor 1975, Boucher 1984, Taylor *et al.* 1985), indicates however, that they have re-established all essential mutualistic relationships and survived interactions with resident competitors and predators (Kruger *et al.* 1986, Crawley 1987). The species have the advantages of being pre-adapted to climatic and edaphic conditions in South Africa and of having escaped their suite of predators and parasites (Milton 1980; see van den Berg 1980a,b,c for information on associated seed predators and herbivores in Australia).

In terms of niche theory (Colwell & Fuentes 1975) one would predict that these alien species have experienced 'ecological release' which may be expressed as enhanced growth or reproductive output in the country of introduction. This in turn, may lead to 'niche expansion' i.e. the occupation of a larger proportion of the species' fundamental niche relative to that in the country of origin. The extent of niche expansion would depend upon the outcome of competitive interactions with indigenous species along the invasive front.

Although at this stage it is not possible to measure whether niche expansion has occurred in alien *A. saligna* and *A. cyclops*, firstly because of a lack of comparative data from Australia and secondly because of the incomplete historical record of introduction and establishment in South Africa, some circumstantial evidence exists in its support. Despite a similar magnitude of *A. cyclops* seed production in Australia and South Africa, the ratio of seeds stored in the soil to seeds produced is much higher in South Africa (Gill & Neser 1984). No comparative data are available for *A. saligna*, but the very large seed banks measured in South Africa are likely to exceed those in Australia (Milton & Hall 1981). Their high soil-stored seed density in South Africa may allow the aliens to dominate the regeneration niche (Grubb 1977), resulting in the formation of dense stands which are commonly observed. Secondly, both species have established in the Eastern Cape which experiences a non-mediterranean climate, with 30% of annual rainfall occurring in summer (December-February) compared to 3-20% in native habitats (data from Fuggle 1981; Bureau of Meteorology "Climatic Averages Australia" 1969).

These two lines of circumstantial evidence support the hypothesis that ecological release and niche expansion has occurred in South Africa. Although beyond the scope of this present study, a more rigorous test of ecological release would be provided by a comparison of growth rates and net reproductive output in a comparable range of habitats between the two continents.

(d) Importance of seed bank dynamics studies

High seed production in many species does not imply that any variation in numbers is inconsequential (Janzen 1969). Plant abundance in a given area may be strongly influenced by the seed rain (Green & Palmbald 1975), possibly because of the importance of post-dispersal seed mortality and the need to reach as many safe germination sites as possible (Neser & Kluge 1986). Seed mortality accounts for the vast majority of all instances of plant mortality, therefore factors affecting the seed stage may have a profound influence on plant population dynamics and structure (Hanzawa *et al.* 1988). The seed bank has dynamic properties of its own (Harper 1977) and may be a useful population parameter as it is buffered against annual variations in environmental conditions and gives a good measure of long-term trends (Fernandez-Quintanilla 1988). A seed bank is also important for continuation of a species in a given locality and, especially in narrowly endemic species, for maintaining genetic variability and stability (Baskin & Baskin 1978).

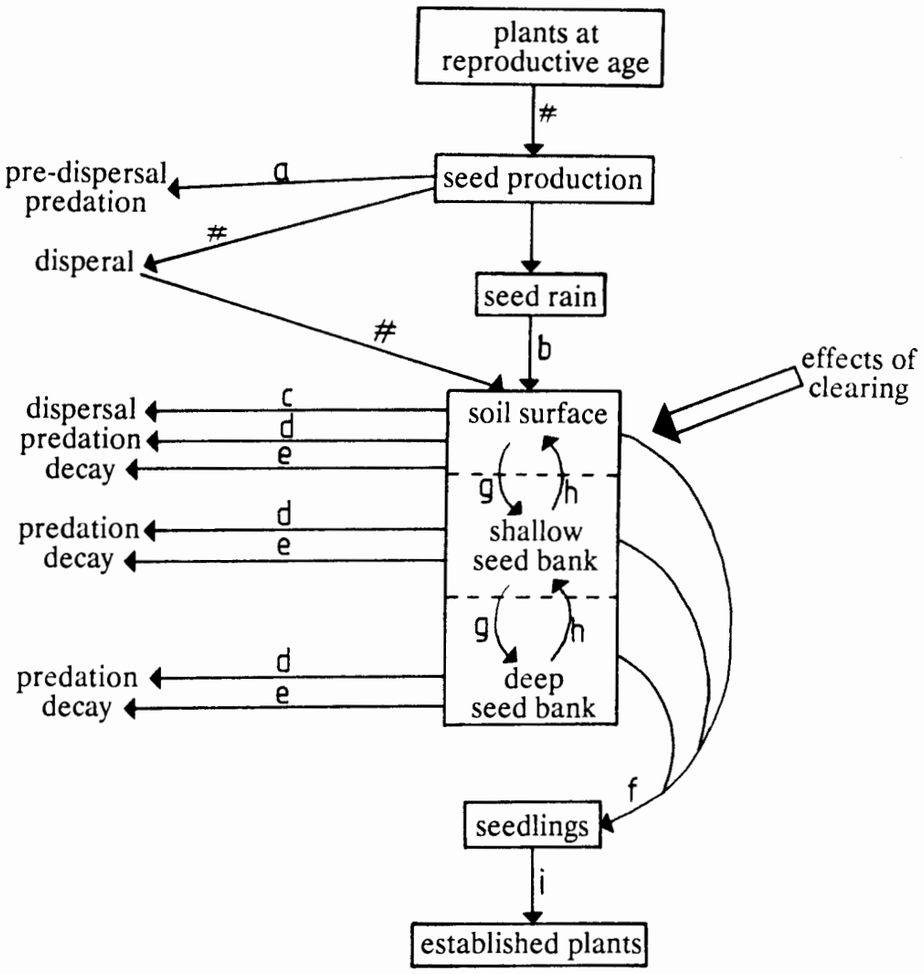
In many studies of weed population dynamics, the behaviour of seeds in the soil emerged as the most important aspect of the life-cycle (e.g. Harper 1965, Chancellor 1968, Egley & Chandler 1978, Zorner *et al.* 1984, Fernandez-Quintanilla 1988). Most studies involved monocarpic species in which the size of future adult populations depends upon factors controlling germination and seedling establishment (Harper 1965). Important factors in weed seed bank dynamics are therefore the maintenance of dormancy and viability through recurring unfavourable seasons (Harper *ibid.*).

The fact that *A. saligna* and *A. cyclops* are fairly long-lived perennials does not necessarily reduce the importance of the seed fraction in their overall population dynamics. Many legume species have become weeds as a result of water-impermeable, seed-coat dormancy (Rolston 1978), which may lead to large numbers of viable seeds accumulating in the soil. Furthermore, many alien plants have displaced indigenes by shading out their reproduction and then occupying the safe sites for germination and seedling establishment (Vitousek *et al.* 1987). In any

case it can be argued that obligate seeders in fire-prone environments (such as fynbos (van Wilgen 1982)) resemble monocarpic species (Sagar & Mortimer 1976, Zammit & Westoby 1987) since adults are killed by fire and recruitment from the seed bank essentially occurs only immediately post-fire. The soil seed bank is thus a critical factor in the reproduction of such species (Keeley 1987). However, the life-cycle of *A. saligna* is complicated by the fact that it may also regenerate by resprouting from damaged trunks.

(e) Theoretical framework

A study of alien *Acacia* seed bank dynamics was pursued because this fraction of the life-cycle appears to be the most important in determining the plants' invasive abilities. The two approaches adopted were a simple monitoring of seed bank changes over several years following the removal of adult plants, and a demographic study of the passive (seed bank) phase of the life-cycle and its processes under mature stands and in the open (Figure 1).



	Process	*Paper*
a	predispersal predation	5,6
b	seed rain	7
c	dispersal	7
d	predation	7
e	decay*	8,9
f	germination	2,3,9
g	burial	10
h	uplift	10
i	seedling survival	3

outside the scope of this study

* includes loss of viability, pathogenic attack and pre-emergence mortality in germinated seeds

Figure 1. An overview of the scope of the study, summarizing the major processes in Acacia seed bank dynamics

Although much seed bank data have been published internationally, both from community-based studies and weed seed demography (Harper 1977, Cook 1980, Roberts 1981) very few general hypotheses pertaining to seed banks have emerged. However, three are pertinent to the present study:

(i) *Seed bank size* Buried seed density is correlated positively with disturbance and negatively with stress (at an evolutionary level) (Thompson 1978). Thus for obligately seeding species, large seed banks would be predicted to accumulate in communities periodically disturbed (e.g. by fire), and small seed banks in communities in which some constraint of the environment severely limits the rate of dry matter production.

Most of Southwestern Australia comprises nutrient-deficient soils (Beard 1983), and similarly, fynbos vegetation occurs on soils deficient in nutrients, particularly nitrogen and phosphorus (Kruger et al. 1983). On the basis of disturbance regime and nutrient stress in native habitats, large and small seed banks, respectively, would be predicted for both *Acacia* species. However, the presence of root nodules (Hoffman & Mitchell 1986) which may fix nitrogen (Roux & Warren 1963), and the infection of roots with vesicular-arbuscular mycorrhizal fungi which may enhance phosphorus uptake (Hoffman & Mitchell 1986), give these legume species the potential to overcome the major nutrient limitations of their environment, which may not be possible for co-occurring non-legume species. Therefore on balance, one would predict both *Acacia* species to maintain relatively large, persistent seed banks in the soil.

(ii) *Types of seed bank* Although each species has its own type of seed bank in terms of longevity patterns and germination responses at different times of year (Grime 1979), four major types of seed bank have been identified (Thompson & Grime 1979): Types I and II are transient, being adapted to exploit gaps created by seasonally predictable damage and mortality in the vegetation; Type III contains some seeds which germinate soon after release and others which persist in the soil for at least a year; and Type IV is persistent as it contains predominantly dormant seeds, promoting regeneration in communities where disturbance of the established vegetation is temporally and/or spatially

unpredictable. However, Grubb (1988) recognises an important dichotomy in persistent seed banks: between those in which germination is coupled to disturbance events (e.g. fire) and those in which germination is uncoupled to disturbance events and is "risk-spreading". The first extreme encompasses Type IV seed banks, as large dormant seed banks accumulate between disturbances, but the latter extreme may not be entirely equivalent to the Type III seed bank, as the extent of its seed bank is extremely variable. Since the *Acacia* species both experience unpredictable disturbance events in their native communities, one would predict them to possess a Type IV, or "disturbance-coupled" seed bank.

(iii) *Seed bank decay* Seed populations in the soil have a continuous and constant death risk which may be described by a negative exponential equation (Roberts 1972, Cook 1980):

$$N = No.\exp(-gt),$$

where N is the population size at time t, No is the initial population size and g is a constant decay rate for a particular set of environmental conditions. More recently, however, Lonsdale (1988) has argued that as for seedlings and plants, survivorship in seeds may encompass all three basic curves (i.e. Deevey Types I, II and III).

In addition to the above, two further general hypotheses are proposed:

(iv) Assuming the seed bank to be the critical phase of the life-cycle, it is predicted that the same seed bank processes will provide the key to invasive potential in the two species, since they have invaded similar fynbos communities.

(v) As fynbos communities are periodically disturbed by fire, it is predicted that factors which promote seed accumulation in the soil (notably high seed longevity) and a rapid germination response in the immediate post-fire environment (heat-stimulated germination) will be the key processes leading to invasive success.

Within the above theoretical framework, several assumptions are tested (pertinent papers are listed in parentheses):

(i) Soil-stored *Acacia* seeds have a high percentage viability and a high level of seed-coat imposed dormancy (2,9).

(ii) *Acacia* seeds have a long life-span in the soil (1,8,9).

(iii) High percentage viability and dormancy relate to an absence of pre-dispersal seed predators (notably seed-sucking insects) (5,6).

(iv) Large seed banks have accumulated because of low levels of predation and dispersal (6,7).

(v) *Acacia* seeds are stimulated to germinate by dry heat treatment (4).

(vi) Clearing of the parent stand by burning methods results in a greater reduction in soil-seed density than by felling alone (1,3).

II RESEARCH FINDINGS

(a) Effects of clearing treatment

Paper 1. Holmes P.M., Macdonald I.A.W & Juritz J. 1987. Effects of clearing treatment on seed banks of the alien invasive shrubs *Acacia saligna* and *Acacia cyclops* in the southern and south-western Cape, South Africa. J. Appl. Ecol. 24:1045-1051.

Paper 2. Holmes P.M. 1988. Implications of alien *Acacia* seed bank viability and germination for clearing. S. Afr. J. Bot. 54:281-284.

Paper 3. Holmes P.M. 1989. The effect of different clearing treatments on the seed bank dynamics of an invasive Australian shrub *Acacia cyclops* in the south-western Cape, South Africa. For. Ecol. Man. 28:33-46.

Paper 4. Jeffery D.J., Holmes P.M. & Rebelo A.G. 1988. Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. S. Afr. J. Bot. 54:28-34.

Journal of Applied Ecology (1987), **24**, 1045–1051

EFFECTS OF CLEARING TREATMENT ON SEED BANKS OF THE ALIEN INVASIVE SHRUBS *ACACIA SALIGNA* AND *ACACIA CYCLOPS* IN THE SOUTHERN AND SOUTH-WESTERN CAPE, SOUTH AFRICA

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SUMMARY

(1) Populations of buried viable seeds of *Acacia cyclops* and *A. saligna*, invasive aliens of fynbos, were estimated to assess the effects on them of different shrub-clearing treatments.

(2) Seed populations of both species declined significantly after 1 year with burning, but in general, not thereafter.

(3) Seed banks of *A. cyclops*, but not of *A. saligna*, were reduced by shrub felling alone after 1 year, apparently because a high proportion of seeds do not have seed-coat induced dormancy, and thus germinate immediately.

INTRODUCTION

The fynbos biome is famous for the richness and diversity of its plant species (Bond & Goldblatt 1984). Fynbos communities are highly susceptible to invasion by alien trees and shrubs (Macdonald 1984). Two of the most important invaders are *Acacia saligna* (Labill.) Wendl. and *A. cyclops* A. Cunn. ex G. Don (Macdonald & Jarman 1984). Alien *Acacia* species are widely distributed, often at high density (Hall & Boucher 1977; Macdonald, Jarman & Beeston 1985). Conservation of fynbos requires the control of these and other alien woody species, which is expensive (Macdonald, Jarman & Beeston 1985).

Annual seed production by *A. saligna* and *A. cyclops* is about 10000 and 3000 seeds per 1 m^2 of canopy cover, respectively (Milton & Hall 1981). Seeds can be bird-dispersed (Glyphis, Milton & Siegfried 1981), but most fall directly to the ground. A large proportion remains dormant, because of a water-impermeable testa (Rolston 1978), resulting in the accumulation of large seed banks in the soil. Heat rupture of the lens (a specialized area of the seed coat in legumes) allows imbibition and breaks dormancy (Tran & Cavanagh 1984). Australian *Acacia* species establish following fire (Floyd 1976) and in South Africa develop into dense thickets.

Many legumes have become weeds as a result of large numbers of viable seeds persisting in the soil (Rolston 1978). Seed bank reduction thus provides a potential key to successful control of invasive alien acacias. This paper investigates the effects of different shrub-clearing treatments on alien *Acacia* seed banks.

METHODS

Selection of study areas

Ten sites (all those available to us) with a long history of infestation by *Acacia*, dense current infestation and well-documented past management were studied (Table 1). Each

TABLE 1. Location and description of study sites

Site		Location	Altitude (m)	Mean annual rainfall (mm)	Geology and soil	Indigenous vegetation community*	*Acacia* species studied	Approximate age of stand (years)
1	Penhill	Cape Flats 33°59′S 18°43′E	20	535	Deep recent sands	Sand plain fynbos	*A. saligna*	30
2	Grootphisantekraal	Durbanville 33°48′S 18°41′E	100	550	Clays on malmesbury shale	Renosterveld	*A. saligna*	25
3	Buffels Bay	CGHNR† 34°19′S 18°41′E	60	450	Deep recent sands	Strandveld/mountain fynbos	*A. saligna*	25
4	Silvermine Nature Reserve	Muizenberg 34°05′S 18°27′E	100	750	Shallow sand over sandstone	Mesic mountain fynbos	*A. saligna*	25
5	Cape Flats Nature Reserve	Cape Flats 33°56′S 18°37′E	65	535	Deep recent sands	Strandveld/sand plain fynbos mosaic	*A. saligna*	50
6	Goukamma Nature Reserve	Sedgefield south Cape 34°03′S 22°57′E	20	750	Deep recent sands	Dune fynbos/kaffrarian thicket mosaic	*A. cyclops*	45
7	Buffels Bay	CGHNR† 34°19′S 18°27′E	50	450	Deep recent sands	Strandveld	*A. cyclops*	80
8	Rondevlei Nature Reserve	Cape Flats 34°03′S 18°29′E	30	664	Deep recent sands	Strandveld	*A. cyclops*	35
9	Walker Bay Forest Reserve	Hermanus 34°25′S 19°24′E	20	725	Deep recent sands	Strandveld	*A. cyclops*	40
10	Potbank	CGHNR† 34°19′S 18°25′E	10	400	Deep recent sands	Strandveld	*A. cyclops*	40

* From Moll *et al.* (1984).
† Cape of Good Hope Nature Reserve.

TABLE 2. The effects of clearing treatments on *Acacia saligna* seed banks (mean number of viable seeds $m^{-2} \pm$ S.E., sample size in parentheses)

Site & clearing treatment	Before treatment	Treatment	Years elapsed since treatment applied 1	2	3	4	5	6	7	8
1 Fell only	10400* ±1870 (50)	Fell	9850* ±3150 (50)	—	—	—	—	2090† ±250 (50)	—	—
2 Fell only	45800 ±3230 (50)	Fell	46800 ±3650 (50)	—	—	—	—	—	—	—
3 Fell, pile & burn piles	13200 ±1000 (60)	Burn pile	—	—	—	0† ±0 (20)	—	—	—	—
		Fell only	—	—	—	2140† (20)	—	—	—	—
4 Fell & burn	7920 ±560 (25)	Burn	—	83† ±21 (25)	15 ±6 (20)	— (20)	9 ±3	—	7 ±2 (25)	—
5 Fell & burn	22400 ±2310 (60)	Burn	2190*† ±350 (100)	1180* ±390 (14)	—	—	—	—	—	1240 ±160 (60)

* Data from Milton & Hall (1981).
† Significant reduction in seed bank (by Z-test, $P < 0{\cdot}01$) compared to previous density.

site had previously been subjected to a shrub-clearing programme, which involved felling, stacking and burning treatments in various combinations (Tables 2 and 3), with subsequent repeated control of germinants to prevent further direct seed input.

Sampling methods

Densities of buried seeds were estimated in 1985 before and after clearing treatments. Three sites previously studied by Milton & Hall (1981) were just resampled. The other sites were chronosequences having a range of clearing dates. Aerial photographs were used to confirm the prior homogeneity of infestations at these sites and the maximum distance between sampling plots was 500 m. Although the original seed banks are unlikely to have been homogeneous across the chronosequences, only mature stands were selected to minimize seed bank variability, and the results obtained from the two approaches show the same order of response to specific treatments.

At all sites one 25 m^2 plot was located, subjectively at the chronosequence sites in areas of similar microtopography and different ages since clearing, or at the previously sampled sites. In each plot twenty to sixty soil cores, 5 cm diameter by 15 cm deep, were extracted at random, except at site 8 where a rocky substratum precluded coring. Here all the soil above the rock was collected from twenty to twenty-five 625 cm^2 quadrats. Samples were sieved through 2 mm mesh in the field and *Acacia* seeds extracted.

Seeds were surface-sterilized by washing in a 3·5% sodium hypochlorite solution, and seed-coat impermeability broken by micropylar chipping to ensure the fastest possible germination response (McDowell & Moll 1981). Three replicates of fifty seeds each per plot were placed on moist filter paper in covered Petri dishes and incubated in a growth chamber at 20–25 °C with a 12 h photoperiod of 470 microEinsteins m^{-2} s^{-1} from fluorescent tubes. Seeds were deemed to have germinated when radicles emerged by 1 mm

TABLE 3. The effects of different clearing treatments on *Acacia cyclops* seed banks (mean number of viable seeds $m^{-2} \pm$ S.E., sample size in parentheses)

Clearing treatment	Before treatment	Treatment	Years elapsed since treatment applied 1	2	3	4	6	8	9	12
6 Fell, stack in rows	1370 ±134 (179)	Brash row	258† ±43 (60)	—	—	423 ±79 (39)	544 ±106 (60)	788 ±143 (60)	—	974 ±149 (60)
		Clear lane	211† ±30 (60)	—		312 ±96 (60)	201 ±60 (40)	301 ±70 (60)	—	446 ±115 (40)
7 Fell, pile, burn piles	3650 ±331 (60)	Burn pile	466† ±98 (40)	116† ±33 (40)	93 ±30 (40)	—	—	—	—	—
		Fell only	796† ±193 (40)	410 ±72 (40)	387 ±87 (20)	—	—	—	—	—
8 Fell, pile, burn piles	1430 ±142 (60)	Burn pile	0† ±0 (20)	—	—	—	—	—	25 ±25 (20)	—
		Fell only	336† ±76 (20)	—	—	—	—	—	76 ±41 (20)	—
8* Fell, pile, burn piles	1400 ±294 (50)	Burn pile	102† ±37 (50)	—	—	—	—	—	—	—
		Fell only	833† ±300 (50)	—	—	—	—	—	—	—
9 Burn live stand	5140 ±281 (219)	Burn	—	—	15† ±12 (60)	—	—	—	—	—
10 Fell, pile, burn area	4250 ±840 (20)	Burn	—	—	—	13† ±13 (40)	—	—	—	—

* Data from Milton & Hall (1981).
† Significant reduction in seed bank (by Z-test, $P < 0{\cdot}01$) compared to previous density.

or more and were counted for 2 weeks, by which time all viable seeds were considered to have germinated (Tran & Cavanagh 1984).

Data analysis

Differences in estimated buried seed populations with time were examined by t-testing of linear regression equations (Zar 1974), and differences with treatment by Z-testing (Underhill 1981). Site differences in seed viability were tested using the randomization test for two independent samples (Siegel 1956). A logistic regression model ($\log \frac{\pi}{1-\pi} = -1{\cdot}147 + 0{\cdot}332t$, where π = probability of a viable seed and $t > 0$ years since felling) was fitted to the *A. cyclops* seed viability data from site 6 against time since clearing, using GLIM (Baker & Nelder 1978).

RESULTS

Stopping the seed rain by felling had no effect on *Acacia saligna* seed banks after 1 year, but after 4–6 years they declined by 80%. Felling followed by burning decreased seed

density by 90% after 1 year and by over 94% after 7–8 years (Table 2). The lowest seed density recorded was seven seeds m^{-2} 7 years after felling and burning (site 4). On part of site 4 where felling and burning had occurred, but where follow-up control of germinants had not been done, the developing stand had restored the seed bank to its original size (7140 ± 570 seeds m^{-2}) within 7 years. Germination trials indicated high percentage viability of *A. saligna* seeds remaining in the soil (86–100%), with no significant differences between sites or clearing treatments ($P > 0{\cdot}05$).

Acacia cyclops seed banks declined exponentially after clearing, with greatest reduction in the first 1–2 years ($P < 0{\cdot}01$) and little thereafter (Table 3). Where sites were partially burnt (sites 7 and 8), seed densities were lower under burnt piles than in felled but unburnt areas ($P < 0{\cdot}01$). Similarly, the seed densities at site 6 were lower where brush was cleared ($P < 0{\cdot}01$) than under the brush rows. Germination trials indicated a large range in percentage viability of *A. cyclops* seeds between sites (46·0–95·3%), with site 9 the highest ($P < 0{\cdot}05$). Percentage viability of soil-stored seeds increased significantly with time elapsed since clearing at site 6 ($\chi^2 = 20{\cdot}91$, $P < 0{\cdot}0001$).

DISCUSSION

Although long-term monitoring of sites is more likely to produce accurate data on seed bank decline following clearing than using chronosequences, adopting both approaches at site 8 gave us no difference. Buried viable seed density did not increase under standing thicket during 5 years between Milton & Hall's (1981) and our studies, which indicates that seed bank equilibrium had been reached prior to clearing. The number of soil samples extracted to estimate seed bank densities under closed *Acacia* canopies was adequate, as the standard error of the mean lay between 7 and 20% (Thompson 1986). However, where seed density was greatly reduced by clearing treatment, remaining seeds had a highly clumped distribution, resulting in higher standard errors.

Burning appeared to kill about 90% of the buried viable seed population but also exposed seeds and thus probably facilitated germination (Kruger & Bigalke 1984; Milton & Hall 1981) and the development of new stands.

The small annual decrease in *A. saligna* seed banks with felling, may be largely the result of predation. Less than 4% of buried *A. saligna* seeds germinate without treatment to the testae (Milton & Hall 1981), whilst decay rates, though unknown, may be low in dry, sandy substrata. However, the striped field mouse (*Rhabdomys pumilio*) consumes 19–40% of seeds present in the litter layer of mixed *Acacia* stands (David 1980), while gerbils (*Tatera afra*) and several bird species also actively forage for *Acacia* seeds (Glyphis, Milton & Siegfried 1981; Pieterse 1984).

Seed populations of *A. cyclops* declined exponentially, with over 50% reduction in the first year. By contrast, after felling only, *A. saligna* seed banks declined similarly to the pattern found for annual weed seeds in undisturbed soil (Roberts & Feast 1973), where the mean decrease was 12% per year. The difference seems to be because *A. cyclops* produces fewer seeds with impermeable testas (Rolston 1978). Germination rates of untreated *A. cyclops* seeds are three times those of *A. saligna* (Milton & Hall 1981). Thus, a greater proportion of the seed bank may be lost due to germination in *A. cyclops* than in *A. saligna*.

Irrespective of clearing treatment, enough seeds always remained in the soil to regenerate new *Acacia* stands. Any programme of *Acacia* shrub clearance must therefore always include subsequent treatment to kill seedlings.

Burning reduced *A. saligna* and *A. cyclops* seed banks more than clearing without burning and thus we recommend burning in fire-adapted fynbos (van Wilgen 1982). However, since *A. cyclops* is predominantly an invader of coastal fire-sensitive vegetation and because its seed banks declined rapidly in the absence of burning, fire may be an inappropriate tool here.

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Implications of alien *Acacia* seed bank viability and germination for clearing

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Percentage viability of *A. saligna* and *A. cyclops* seed banks was determined for stands cleared of mature plants for different time intervals. Seedling emergence following recent clearing was monitored for a year at one site of each species. Percentage viability of *A. saligna* seed banks was uniformly high and was not affected by age since clearing. Percentage dormancy in *A. saligna* was high since few seedlings emerged in the field (1% of viable seed bank), but after fire, 70% of the remaining viable seed bank germinated. Percentage viability of *A. cyclops* seed banks differed significantly among sites, with the proportion of viable seeds in the soil increasing significantly with age since clearing at one site. Percentage germination and viability of fresh *A. cyclops* seeds also differed significantly among sites. Although seedling emergence in *A. cyclops* (9% of viable seed bank) exceeded that in *A. saligna*, pre-emergence mortality was implicated as the more important process in *A. cyclops* seed bank decline. In order to markedly reduce seed banks, it is recommended that *A. saligna* stands should be burnt and *A. cyclops* stands cleared in any way which removes the vegetation cover.

Die persentasie kiemkragtigheid van *A. saligna*- en *A. cyclops*-saad in die grond is bepaal vir stande waarvan die volgroeide plante op verskillende tydsintervalle verwyder is. Die verskyning van kiemplante na die vorige ontbosting, is vir 'n periode van 'n jaar op een perseel vir elk van die spesies aangeteken. Die persentasie kiemkragtigheid van *A. saligna*-saad in die grond was deurgaans hoog en was nie deur ouderdom, sedert die vorige ontbosting beïnvloed nie. Die persentasie rustende saad by *A. saligna* was baie hoog aangesien slegs enkele kiemplante in die veld hul verskyning gemaak het (1% van die kiemkragtige saad), maar na 'n brand, het 70% van die oorblywende kiemkragtige saad in die grond ontkiem. Die persentasie kiemkragtigheid van *A. cyclops*-saad in die grond het aansienlik van perseel tot perseel verskil, met 'n toename in die verhouding kiemkragtige saad met verloop van tyd na ontbosting. Die persentasie ontkieming en kiemkragtigheid van vars *A. cyclops*-saad het ook aansienlik van een perseel na die ander verskil. Alhoewel die verskyning van saailinge by *A. cyclops* (9% van kiemkragtige saad) in die grond dié van *A. saligna* oortref, word geïmpliseer dat die afsterf van kiemplante voor dit bo die grond verskyn, as die belangrikste oorsaak vir die afname van *A. cyclops*-saad in die grond is. Ten einde die saadvoorraad in die grond aanmerklik te verlaag, word daar aanbeveel dat *A. saligna*-stande gebrand word en *A. cyclops*-stande ontbos word op so 'n wyse dat die plantbedekking verwyder word.

Keywords: *Acacia cyclops, Acacia saligna*, alien, seed germination, seed viability

Introduction

The alien invasive species, *A. saligna* (Labill.) Wendl. and *A. cyclops* A. Cunn. ex G. Don, were introduced into South Africa from Australia in the mid-nineteenth century (Shaughnessy 1980). These two species accumulate large seed banks in the soil which pose a major obstacle to their successful control (Holmes *et al.* 1987b). Viability of fresh seed of *A. saligna* and *A. cyclops* usually exceeds 90% (Jones 1963; Jeffery *et al.* 1988) but little is known of the effects of storage time in the soil. *Acacia* seeds typically have a 'hard' water-impermeable seed-coat, which enables them to remain dormant in the soil for extended periods, in some cases up to 50 years (Cavanagh 1980). Seed viability and dormancy are major determinants of seed persistence in the soil (Harper 1977). Knowledge of these may allow an evaluation of the effectiveness of stand-clearing treatments in reducing populations of alien acacias. This paper reports on percentage viability of seed banks in areas cleared of *A. saligna* and *A. cyclops* for different periods and seedling emergence in recently cleared stands.

Methods

Acacia saligna and *A. cyclops* seed bank viability was determined at nine different sites throughout the Cape (Table 1), while seedling emergence after clearing was monitored at two of the sites (viz. Schustersrivier and Buffels Bay). Each site provided areas which had been cleared in different years of dense, mature *Acacia*, using a particular treatment (either felling, burning or a combination of both; Holmes *et al.* 1987b) and regularly weeded of re-establishing acacias. In each different area, seeds were extracted from 20–25 random soil cores (15 cm deep by 5 cm diameter).

Seeds were sieved from the cores, surface-sterilized by washing in a 3,5% sodium hypochlorite solution, and seed-coat impermeability broken by micropylar chipping (McDowell & Moll 1981). From each area, three replicates of 50 seeds each were placed on moist filter paper in covered petri dishes and incubated in a growth chamber at 20–25°C with a 12-h photoperiod of 470 μEinsteins $m^{-2}\,s^{-1}$ from fluorescent tubes. Seed viability was taken to be the proportion of germinated seeds (as determined by 1-mm radical extension) after 2 weeks germination. All non-viable seeds rotted within a 2-week period. Because of high inter-site variation in the viability of *A. cyclops* seed banks, fresh seeds of this species were harvested and tested for spontaneous germination and viability. Five replicates of 25 seeds each were prepared as above and allowed to germinate over a period of 4 weeks, before chipping them to determine their percentage viability.

Seedling emergence of *A. saligna* and *A. cyclops* was monitored over a year following the felling and clearing of two separate stands in July 1985 at Cape Point. Seedlings were counted at 2-monthly intervals in five randomly located, permanent plots (0,25 m^2 and 0,5 m^2 for *A. saligna* and *A. cyclops*, respectively). Seedlings were tagged in order to monitor emergence and mortality, and the number of seedlings with mature leaves (i.e. phyllodes, which develop from 8 weeks) was also monitored.

Differences in percentage germination and viability among sites were analyzed by generalized linear models (GLIM; Baker & Nelder 1978). Null models with binomial

Table 1 Location and description of study sites

Site	Location	Geology	Indigenous vegetation community[1]	*Acacia* species studied	Stand age before clearing (years)
1 Penhill	Cape Flats 33°59'S 18°43'E	Deep recent sands	Sand plain fynbos	*A. saligna*	30
2 Grootphisante-kraal	Durbanville 33°48'S 18°41'E	Clays on malmesbury shale	Renosterveld	*A. saligna*	25
3 Schustersrivier	CGHNR[2] 34°12'S 18°24'E	Deep recent sands	Mountain fynbos	*A. saligna*	25
4 Silvermine Nature Reserve	Muizenberg 34°05'S 18°27'E	Shallow sand over sandstone	Mesic mountain fynbos	*A. saligna*	25
5 Cape Flats Nature Reserve	Cape Flats 33°56'S 18°37'E	Deep recent sands	Strandveld/sand plain fynbos mosaic	*A. saligna*	50
6 Goukamma Nature Reserve	Sedgefield south Cape 34°03'S 22°57'E	Deep recent sands	Dune fynbos/ kaffrarian thicket mosaic	*A. cyclops*	45
7 Buffels Bay	CGHNR 34°19'S 18°27'E	Deep recent sands	Strandveld	*A. cyclops*	80
8 Rondevlei Nature Reserve	Cape Flats 34°03'S 18°29'E	Deep recent sands	Strandveld	*A. cyclops*	35
9 Walker Bay Forest Reserve	Hermanus 34°25'S 19°24'E	Deep recent sands	Strandveld	*A. cyclops*	40

[1]*Sensu* Moll *et al.* 1984
[2]Cape of Good Hope Nature Reserve

Table 2 Mean percentage viability of *A. saligna* and *A. cyclops* seed banks (± *S.E.*) before and after different stand-clearing treatments

Site	Species	Before treatment	Treatment	Years elapsed since clearing 1	2	3	4	6	8	12
1	*A. saligna*	94,0[1]	felled	97,0[1]	–	–	–	100,0 ±0,0	–	–
2	*A. saligna*	95,4 ±1,4	felled	96,0 ±1,2	–	–	–	–	–	–
3	*A. saligna*	98,0 ±1,1	felled	–	–	100[2]	–	–	–	–
4	*A. saligna*	97,3 ±1,3	felled & burnt	–	96,7 ±1,5	–	96,0[2]	–	–	–
5	*A. saligna*	98,7 ±0,9	felled & burnt	86,2[1] ±2,1	–	–	–	–	95,3 ±1,7	– –
6	*A. cyclops*	64,0 ±3,9	felled	30,7 ±3,8	–	–	54,0 ±4,1	72,0 ±4,5	80,7 ±3,2	94,7 ±1,8
7	*A. cyclops*	46,0 ±4,1	felled	53,0[2]	–	60,7 ±4,0	–	–	–	–
8	*A. cyclops*	89,0[1]	felled burnt	78,0[1] 94,0[1]	–	–	–	–	–	–
		72,0 ±4,5	felled	–	–	–	–	–	[3]	–
9	*A. cyclops*	95,3 ±1,7	burnt	–	–	85,3[2]	–	–	–	–

[1]Data from Milton & Hall 1981
[2]Insufficient seed available for replication (n = 1 batch of 50 seeds). In all other cases n = 3 batches of 50 seeds
[3]Insufficient seeds for testing
The logistic model fitted to the site 6 seed viability data against time was: $\log [\pi/(1-\pi)] = -1{,}147 + 0{,}332t$, where π = probability of a viable seed and $t > 1$ year. Percentage seed viability increased significantly with time elapsed since clearing ($\chi^2 = 20{,}91$; $P < 0{,}0001$)

errors and logit functions were fitted to the data, then parameters were added to account for the effects of site and replication. Overall significance of effects was established by examining reductions in deviance (distributed as Chi-square) relative to those of the null models. Where the overall effect of site was significant, differences between sites were further compared by fitting models which allowed for certain sites to be the same. The best fitting model was selected using the Chi-squared goodness of fit statistic, the model being accepted if deviance $< \chi^2_{df}$ ($P = 0,05$). A logistic regression model was used to test the effect of time on percentage seed viability at one site (Goukamma).

Results

Viability of *A. saligna* seed banks ranged from 86,2% to 100% with no significant differences ($P > 0,05$) between sites, clearing treatments or ages since clearing (Table 2). Viability of *A. cyclops* seed banks varied significantly between sites before treatment ($P < 0,01$, range 46,0–95,3%; Table 2). No clearing effect was determined (between site comparison), but at Goukamma, percentage viability of seed banks increased significantly with age since clearing ($\chi^2 = 20,91$, $P < 0,0001$).

Analysis using GLIM on percentage germination of fresh *A. cyclops* seeds yielded two equally acceptable models: viz. significant differences between all sites [deviance $< \chi^2_{16}$, ($P = 0,05$)] or Goukamma and Rondevlei had the same percentage germination (Table 3). Similarly for percentage viability of fresh *A. cyclops* seeds two equally acceptable models resulted: viz. significant differences between all sites or Buffels Bay and Rondevlei had the same percentage viability.

Seedling emergence following felling in *A. cyclops* was about twice that in *A. saligna* (Table 4). Very few seedlings of either species emerged in the summer months (November–March) and mortality of non-phyllode seedlings was especially high during this period. Seed banks contained 3 650 viable seeds m^{-2} (*A. cyclops*) and 13 200 viable seeds m^{-2} (*A. saligna*) prior to clearing (Holmes *et al.* 1987b), thus in the first 6–8 months after clearing, a minimum of 8,73% and 1,37% of the viable seed bank germinated in *A. cyclops* and *A. saligna*, respectively. Following an accidental summer fire at the *A. saligna* site, its seed bank decreased to 932 ± 94,1 ($\bar{x} \pm S.E.$, n=60 cores) uncharred seeds m^{-2} of which 33,3 ± 12,5% of the seeds were dead and a further 30,0 ± 9,5% germinated within 4 weeks (i.e. were non-dormant). In total, therefore, 95% of the *A. saligna* seed bank was killed by the fire. Based on the non-dormant seed bank fraction, 280 ± 154 seedlings m^{-2} would be predicted to germinate following the first rains. Within 6 months of the fire, 436 seedlings m^{-2} had emerged (Table 4), leaving an estimated seed bank of 185 seeds m^{-2} (or 1,4% of the original seed bank).

Table 3 Percentage germination and viability (Mean ± *S.E.*, n=5) of fresh *A. cyclops* seeds from different sites

Site	% germination at 4 weeks	% viability
6	20,0 ± 4,2	75,2 ± 4,4
7	8,0 ± 2,8	92,8 ± 2,7
8	15,2 ± 3,7	95,2 ± 2,2
9	2,4 ± 1,6	99,2 ± 0,9
Overall effect of site		
	$\chi^2_3 = 25,16$ $P < 0,001$	$\chi^2_3 = 44,17$ $P < 0,001$
Goodness of fit of log-linear models: all sites differ		
	$\chi^2_{16} = 20,89$ $0,1 < P < 0,5$	$\chi^2_{16} = 21,38$ $0,1 < P < 0,5$
	site 6 = site 8 $\chi^2_{17} = 21,52$ $0,1 < P < 0,5$	site 7 = site 8 $\chi^2_{17} = 23,74$ $0,1 < P < 0,5$

Discussion

As percentage viability of *A. saligna* seed banks remained high for several years after clearing, it is probable that buried seeds will remain viable for long periods. The uniformity of *A. saligna* seed viability among sites may reflect the absence of associated seed-feeding insects in South Africa (van den Berg 1980).

Table 4 *Acacia* seedling emergence (mean seedlings m^{-2} ± *S.E.*, n = 5) at Cape Point following felling of mature stands in July. In February, an accidental fire swept through the *A. saligna* site

	A. cyclops			*A. saligna*		
Month	Total seedlings	Phyllode seedlings	New seedlings	Total seedlings	Phyllode seedlings	New seedlings
Sept.	232,4 ±53,0	0,4 ±0,4	232,4 ±53,0	127,2 ±22,8	33,6 ±6,8	127,2 ±22,8
Nov.	118,8 ±17,4	33,2 ±15,4	65,6 ±21,6	75,2 ±25,2	24,0 ±13,2	53,6 ±10,4
Jan.	33,2 ±10,8	22,0 ±10,4	14,0 ±7,4	20,8 ±9,2	20,8 ±9,2	0,0 ±0,0
				Total emergence (before fire) =		180,8
Mar.	23,6 ±12,4	16,8 ±9,6	6,8 ±6,8	10,4 ±7,6	10,4 ±7,6	0,0 ±0,0
		Total emergence =	318,8			
May	*			310,4 ±86,0	13,6 ±6,8	296,8 ±82,0
July	*			179,2 ±32,8	40,4 ±13,6	139,2 ±35,6
				Total emergence (since fire) =		436,0

*Plots disrupted by game animals

The low percentage emergence of *A. saligna* seedlings following clearing (1%) is indicative of the species' high level of seed-coat imposed dormancy (Jeffery *et al.* 1988). Furthermore, this dormancy is readily broken by heat (Jones 1963; Milton & Hall 1981; Jeffery *et al.* 1988) as is illustrated by the seedling flush following the accidental fire: 70% of the remaining viable seed bank germinated in 6 months following the fire. This figure is marginally higher than predicted by the non-dormant fraction, perhaps reflecting the longer germination period in the field than in the germination trials. The proportion of the seed bank killed by fire was similar to that for *A. longifolia* following a felling and burning treatment (Pieterse & Cairns 1986).

Percentage viability of *A. cyclops* seed banks did not decrease with age, thus buried seeds may remain viable for long periods. The high percentage rotting of seeds from under some stands indicates that a large proportion may be damaged [e.g. by alydid bug feeding punctures (Holmes *et al.* 1987a)] and may therefore rot in the soil. The site-inherent differences in germination and viability of fresh *A. cyclops* seeds might reflect genotypic variation, as the degree of hard-seededness varies widely between localities in Australia (Gill 1985). Alternatively, it might be the result of differential exposure to sun or feeding by alydid bugs (Gill 1985; Holmes *et al.* 1987a).

Owing to seed bank losses through germination (non-dormant portion) and rotting (non-viable portion), a large decrease in *A. cyclops* seed banks is predicted for the first year after felling, with a concomitant increase in seedbank viability. In the ensuing years, seed bank viability is expected to remain high, with only a gradual decline in seed density as the few non-viable seeds rot, and some seeds lose dormancy and germinate (Figure 1). However, the observed pattern at Goukamma did not conform to all these predictions (Figure 1). One year after clearing, the proportion of viable seeds in the soil was lower than that under standing thickets, possibly indicating pathogenic attack on soil-stored seeds. The seed bank decreased more than expected in the first year, probably reflecting both the low seed viability and the unmeasured effect of granivory. Six to 12 years after clearing, seed banks did not continue to decline, either indicating spatial heterogeneity in seed banks prior to clearing or a period before which seed-attack by indigenous alydid bugs occurred on *A cyclops* (Holmes *et al.* 1987a). Since there were no fresh inputs of *A. cyclops* after clearing, the latter effect would occur if alydids attack soil-stored seeds under *Acacia* stands, but not in cleared areas.

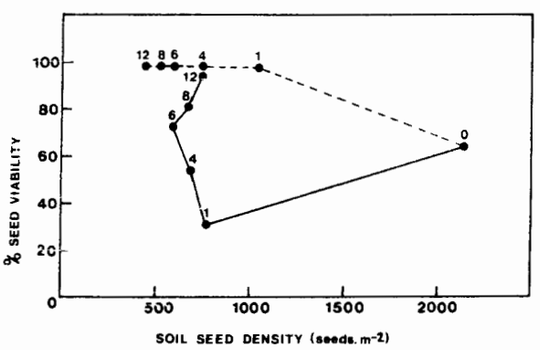

Figure 1 The relationship between total seed bank (seeds m^{-2}, n = 60) and percentage seed viability (n = 3 batches of 50 seeds) for *A. cyclops* at Goukamma. The dashed line is the expected relationship. Years elapsed since clearing of stand are given for each sample.

Acacia cyclops seeds germinate following clearing more readily than those of *A. saligna*. Increasing the exposure time of *A. cyclops* seeds to temperatures attained at bare soil surfaces (viz. 60°C) enhances germination (Gill 1985). Since fire-simulated heat treatment does not increase seed germination in *A. cyclops* so markedly as in *A. saligna* (Jones 1963; Jeffery *et al.* 1988), removal of the vegetation cover is more likely to maximize seed loss through germination than is burning in the former species. In the first year after clearing *A. cyclops* at Buffels Bay, its viable seed bank decreased by 78% (Holmes *et al.* 1987b), of which seedling emergence accounted for only 9%. Contrary to Milton & Hall's (1981) prediction that alien *Acacia* seed bank decline would depend mostly on factors affecting germination, in *A. cyclops* pre-emergence mortality (rotting and predation) appears to be the more important process in the field.

In order to markedly reduce soil-stored seed banks, burning is a necessary treatment for *A. saligna*, whereas in *A. cyclops* any treatment which removes the vegetation cover should maximize seed bank decline.

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Effects of Different Clearing Treatments on the Seed-Bank Dynamics of an Invasive Australian Shrub, *Acacia cyclops*, in the Southwestern Cape, South Africa

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ABSTRACT

Holmes, P.M., 1989. Effects of different clearing treatments on the seed-bank dynamics of an invasive Australian shrub, *Acacia cyclops*, in the southwestern Cape, South Africa. *For. Ecol. Manage.*, 28: 33–46.

Acacia cyclops is an invasive shrub of natural vegetation in the fynbos biome of South Africa. Its large soil-stored seed banks make eradication difficult. In this study, a dense, mature stand of *A. cyclops* was cleared using four commonly applied treatments. Few seeds above 30-mm depth in the soil profile survived burning treatments, and percentage viability was reduced at depths up to 40 mm. Seed germinability was not enhanced by fire. Seedling emergence and mortality, monitored over 13 months post-clearing, were much higher following non-burning and 'fell and burn' treatments than 'burn standing' and 'fell, pile and burn' treatments. Nevertheless, the pattern of seedling emergence and survival was similar in all treatments, with survival low until October, 9 months post-clearing. Although all treatments resulted in significant reductions in seed density 1 year post-clearing, burning treatments were more effective than the non-burning treatment. The 'burn standing' treatment killed more seeds than the 'fell and burn' treatment, and may be recommended where labour costs are prohibitive. Since all treatments induced a rapid seed-bank decline in *A. cyclops*, it is recommended that the choice of treatment be dictated by other factors, such as possible effects on the recovery of indigenous plant species.

INTRODUCTION

Acacia cyclops A. Cunn. ex. G. Don is an evergreen shrub introduced from Australia last century for sand stabilization, shelter-belts and fodder (Shaughnessy, 1980). It is currently the most widespread invader plant in the lowlands of the fynbos biome (Macdonald and Jarman, 1984), and conservation requires its removal.

Acacia cyclops does not resprout after felling or burning (Boucher and Stirton, 1978), relying on seed regeneration. Its invasive ability is partially attrib-

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uted to a prolific production of hard-coated seeds (up to 3000 seeds m^{-2} canopy cover; Milton and Hall, 1981), which are free of their native predators and pathogens (Milton, 1980). In time, *A. cyclops* dominates the soil seed bank, swamping indigenous regrowth when disturbance such as fire creates opportunities for recruitment (Bond and Slingsby, 1984). The high density and putative longevity of its seed banks makes control difficult and expensive (Macdonald and Richardson, 1986).

The water-impermeable dormancy of many *Acacia* seeds can be broken by heat (Tran and Cavanagh, 1984). However, the germinability of *A. cyclops* seeds is not enhanced by dry-heat treatment (Jeffery et al., 1988) in contrast to two other invasive *Acacia* species of fynbos, *A. longifolia* (Pieterse and Cairns, 1986) and *A. saligna* (Jeffery et al., 1988). Thus, while fire has the potential to destroy *A. cyclops* soil-stored seeds, it may not 'flush' surviving seeds by stimulating germination.

In this study, the seed-bank dynamics of *A. cyclops* were investigated at one site in the southwestern Cape Province of South Africa, following the application of four commonly practised clearing treatments. Hypotheses that all treatments would result in significant decreases in seed density, but that burning treatments would be more effective than non-burning treatments 1 year after clearing (Holmes et al., 1987), were tested.

THE STUDY SITE

An isolated stand of dense (5.7 stems m^{-2}), mature (40-year-old) *A. cyclops* at the Walker Bay Forest Reserve (34°19′S, 19°24′E) was studied. The stand

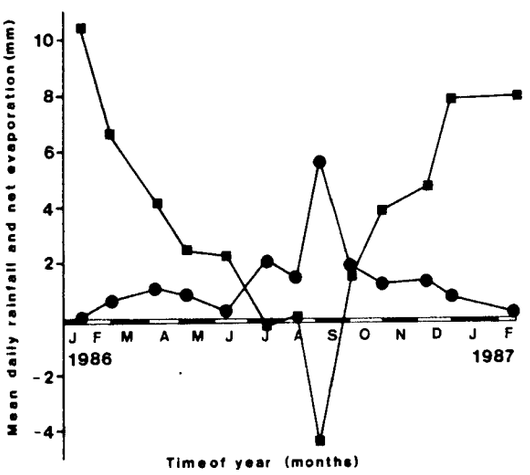

Fig. 1. Mean daily precipitation (●—●) and net pan evaporation (■—■) for the intervals between monthly seedling counts at Walker Bay. Data are from Prinskraal weather station (34°38′S, 20°07′E).

was on deep, aeolian sands inland of the coastal dunes, on a gentle north-facing slope. Prior to stabilization with *A. cyclops*, the area consisted of bare sand bordering Dune Asteraceous Fynbos vegetation (Cowling et al., 1988). The area has a Mediterranean-type climate, with a mean annual rainfall of 539 mm (at Stanford, 10 km east of study site; Fuggle, 1981) and a high probability of summer drought (Fig. 1).

METHODS

Experimental design

The stand was divided into four treatment blocks (Fig. 2). Block 1 was felled and the slash stacked into piles without burning ('fell and pile'), whilst blocks 2–4 received a burning treatment. Block 2 was felled, the slash stacked into piles and the piles burnt ('fell, pile and burn'). Block 3 was burnt standing live ('burn standing'), and block 4 was felled and the whole area burnt ('fell and burn'). Felling was completed in September 1985 and burning was carried out on the first suitable day in January 1986. Conditions during the fire are described in Van Wilgen and Holmes (1986).

Response of buried seeds to burning

Mature *A. cyclops* seeds were collected from randomly selected trees at the Walker Bay Forest Reserve 2 weeks prior to burning. Five replicates, each of approximately 150 seeds, were buried at each of four different depths (10, 20, 30 and 40 mm) at random locations below the soil surface in the 'burn standing' and 'fell and burn' treatments. Buried seeds were placed on fibreglass mesh and the soil and litter replaced to as near natural compaction as possible. Seeds

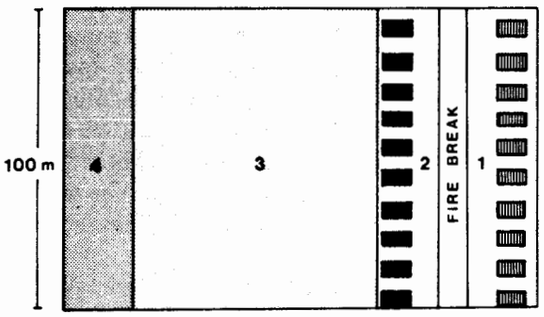

Fig. 2. Experimental layout of four clearing treatments in an *Acacia cyclops* stand at Walker Bay Forest Reserve. Shaded areas received a burning treatment and striped areas represent unburnt slash. Treatments were: (1) 'fell and pile'; (2) 'fell, pile and burn'; (3) 'burn standing'; and (4) 'fell and burn'.

were recovered and examined for charring 24 h after the fire. Uncharred seeds were then tested for germinability (percentage spontaneous germination) and viability, compared to seeds not subjected to fire (controls), by placing seeds in covered petri dishes on filter paper moistened with 6 ml benomyl (0.022% active ingredient; Clemens et al., 1977) and incubating at 25 °C for a 12-h photoperiod alternating with 20 °C in the dark. Seeds were removed when germinated (> 1-mm radicle extension) over a period of 4 weeks, after which ungerminated seeds were considered dormant. Dormant seeds were chipped at the micropylar end to promote imbibition, and those germinating within a further 2 weeks were considered to be viable.

Standard generalized linear models, in which the expected proportions were beta-distributed (Crowder, 1978), were fitted to the data using GLIM (Baker and Nelder, 1978) to test for overall treatment and depth effects.

Seedling emergence and mortality

Following clearing, 20 permanent quadrats of 0.25 m^2 were positioned at regular intervals along two randomly located 10-m transect lines in each treatment. In the 'fell, pile and burn' treatment, two sets of transects were established, one in the burnt piles and the other in clear areas between piles. Total numbers of seedlings, and of seedlings older than 2 months, were counted monthly for 13 months following the fire. Seedlings bear compound leaves for the first 2–3 months following germination, but exclusively develop phyllodes from about 2 months (personal observation, 1986). Minimum total emergence was calculated by summing all juvenile (i.e. non-phyllode) seedlings from every 2nd month. Similarly, minimum mortality was calculated by summing those juvenile seedlings from every 2nd month which were not accounted for in the phyllode stage 2 months hence. These calculations underestimate seedlings which emerge and die within a month. Survival was taken to be the number of phyllode seedlings present at the final count. Numbers of juveniles and total seedlings each month, and estimated seedling mortality, were correlated with mean daily rainfall and net evaporation (standard pan evaporation minus rainfall) for the preceding month, with data from the nearest weather station, Prinskraal (34°38′S, 20°07′E), 60 km east of the study site. Although the mean annual rainfall at Prinskraal is only 367 mm, its cyclonic origin (Fuggle, 1981) probably results in a similar rainfall pattern.

Depth of germination was determined for all treatments except 'fell, pile and burn' by uprooting 100 seedlings at random and measuring hypocotyl length (distance between radicle base and ground level) as an accurate indication of germination depth (Brits, 1987). Median depths of germination for each treatment were compared using the Median test (Siegel, 1956).

Seed banks

Seed density in the soil was estimated prior to clearing in September 1985 by extracting *Acacia* seeds from 50 soil cores (50 mm diameter, 150 mm deep) at random in a 25-m^2 plot for each treatment block. Seed banks were resampled in January 1987. Owing to low seed densities after treatment, a further two randomly located 25-m^2 plots were sampled per treatment. In 'fell and pile' and 'fell, pile and burn' treatments, plots were sampled both under piles and between piles. Seed densities before clearing were compared among treatments using Z tests (Zar, 1974). Owing to significant differences in seed density between certain blocks prior to clearing, percentage reduction figures were used to compare the effectiveness of selected treatments in reducing seed banks, with the Mann-Whitney U Test (Siegel, 1956).

The vertical distribution of seeds in the soil was investigated by excavating successive 40-mm layers from a 0.25-m^2 quadrat, to a depth of 320 mm. This procedure was repeated 1 year after burning for all treatments except 'fell, pile and burn'.

RESULTS

Response of buried seeds to burning

Although weather conditions during the fire were moderate, fire intensities and flame lengths exceeded those recorded under relatively severe conditions in fynbos (Van Wilgen et al., 1985), and soil temperatures exceeded the range anticipated using thermo-chemical indicators: 160°C at 10-mm and 71°C at 40-mm depths (Van Wilgen and Holmes, 1986). Fire intensity, estimated using Byram's (1959) formula $I = Hwr$, was much higher in the 'burn standing' than in the 'fell and burn' treatment (20 000–61 000 versus 9500 kWm^{-1}; H (heat yield) = 18.5 $kJ\ g^{-1}$; w (mass of fuel consumed) = 7687 versus 8590 g m^{-2}; r (rate of spread) = 0.2–0.6 versus 0.06 m s^{-1}; Van Wilgen and Holmes, 1986), probably reflecting a more densely packed fuel bed in the latter, which slows the rate of spread, and thereby the rate of heat release (Van Wilgen et al., 1985). Fire intensity was not calculated for the burning piles as the measure is not valid where residual burning continues long after the passage of the main flame front. In this treatment, the litter layer between piles also burnt completely.

Few seeds in the litter layer and upper 30 mm of soil survived fire (Table 1). Even at 40-mm depth, seed viability in both treatments was significantly lower than that of the control (GLIM: 'burn standing', $\chi^2_1 = 8.26$, $P < 0.005$; 'fell and burn', $\chi^2_1 = 10.65$, $P < 0.003$). Neither seed germinability nor the ratio of germinating to viable seeds was significantly enhanced by fire (GLIM, $P > 0.05$ in all cases).

Burial depth had a significant effect on seed charring, germinability and viability, but there were no treatment or interaction effects (Table 2). Although no overall effect of treatment was detected, charring of seeds at 40 mm depth occurred only in the 'burn standing' treatment (Table 1).

TABLE 1

Effects of burning treatments on *Acacia cyclops* seeds buried at four different depths (10–40 mm) in the soil

Effect	Control (unburnt)	Burn standing				Fell and burn			
		10mm	20mm	30mm	40mm	10mm	20mm	30mm	40mm
Charring	—	100.0 ±0.0	63.9 ±34.7	51.4 ±50.1	9.0 ±16.1	100.0 ±0.0	95.6 ±9.8	56.6 ±35.4	0.0 ±0.0
Germinability	2.4 ±3.6	0.0 ±0.0	5.2 ±7.2	4.4 ±9.8	7.3 ±6.6	0.0 ±0.0	0.0 ±0.0	2.4 ±3.4	11.5 ±9.3
Viability	99.2 ±1.8	0.0 ±0.0	9.2* ±12.6	17.4* ±24.1	38.4* ±33.4	0.0 ±0.0	2.0* ±4.5	9.3* ±13.5	70.1* ±20.5
Germinability/ Viability (G/V)	2.4 ±3.6	0.0 ±0.0	22.8 ±31.5	9.0 ±20.0	21.5 ±20.3	0.0 ±0.0	0.0 ±0.0	20.7 ±21.2	16.7 ±11.6

Data are mean percentages ± SD, $n = 5$ batches of 104–168 seeds; control; $n = 5$ batches of 25 seeds.
*Significantly different from the control (GLIM, $P < 0.05$).

TABLE 2

Deviances obtained from GLIM for effects of depth of burial and burning treatment on *Acacia cyclops* seeds

	df	Deviance (χ^2)	Significance (P-value)
Charring			
Overall effects	4	73.242	<0.001
Treatment effect	1	0.508	>0.250
Depth effect	3	73.236	<0.001
Interaction	3	5.830	>0.100
Germinability			
Overall effects	4	26.972	<0.001
Treatment effect	1	0.560	>0.250
Depth effect	3	29.214	<0.001
Interaction	3	4.576	>0.100
Viability			
Overall effects	4	57.900	<0.001
Treatment effect	1	1.320	>0.250
Depth effect	3	57.440	<0.001
Interaction	3	0.360	>0.900

Seedling emergence and mortality

Seedling emergence and mortality were greatest in the 'fell and pile' and 'fell and burn' treatments, with relatively few emergents in the 'fell, pile and burn' and 'burn standing' treatments (Table 3). In September 1986, 78 ± 61 seedlings m^{-2} ($n = 100$ quadrats of 0.25 m^2) were counted under a neighbouring stand, none with phyllodes. The pattern of seedling emergence, mortality and survival was similar for all treatments (Fig. 3). Seedling survival was low until October 1986, after which it increased (Fig. 3). Monthly counts of juveniles and total seedlings in the 'fell and pile' treatment were negatively correlated with mean daily net evaporation ($r = -0.776$, $P < 0.002$ and $r = -0.645$, $P < 0.009$, respectively). Minimum mortality was also negatively correlated with mean daily net evaporation ($r = -0.570$, $P < 0.05$). The above factors were not correlated with mean daily rainfall (juveniles, $r = 0.279$, $P > 0.3$; total seedlings, $r = 0.217$, $P > 0.4$; mortality, $r = 0.415$, $P > 0.1$).

Treatment had a significant effect on median depth of germination ($\chi^2_2 = 44.34$, $P < 0.001$). Seedlings in the 'fell and burn' treatment emerged from greater depths than those in the 'fell and pile' treatment ($\chi^2_1 = 6.13$, $P < 0.05$), and those in the 'burn standing' treatment from greater depths than in the 'fell and burn' treatment ($\chi^2_1 = 11.84$, $P < 0.01$; Fig. 4).

Seed banks

Prior to clearing the *Acacia* stand, seed density in the soil ranged from 2800 to 7800 seeds m^{-2}, with significant differences between certain blocks (Z-test, $P < 0.05$; Table 4). One year after clearing, seed densities were significantly lower in all treatments, with mean percentage reduction ranging from 80.3% in the 'fell and pile' treatment to 99.9% under burnt piles. Combined results of

TABLE 3

Minimum estimates of total *Acacia cyclops* seedling emergence, mortality and survival (mean number of seedlings $m^{-2} \pm$ SE, $n = 20$ quadrats of 0.25-m^2) for the year following different clearing treatments

	Fell and pile	Fell, pile and burn		Burn standing	Fell and burn
	Clear area	Burnt pile	Clear area		
Emergence	359.2 ± 87.6	8.2 ± 3.5	61.2 ± 17.8	15.4 ± 4.9	371.8 ± 78.1
Mortality	306.8 ± 83.2	6.6 ± 3.5	59.0 ± 17.8	8.6 ± 3.4	295.4 ± 62.8
Survival	50.4 ± 9.6	1.6 ± 0.9	2.2 ± 0.8	6.8 ± 2.0	74.8 ± 21.2

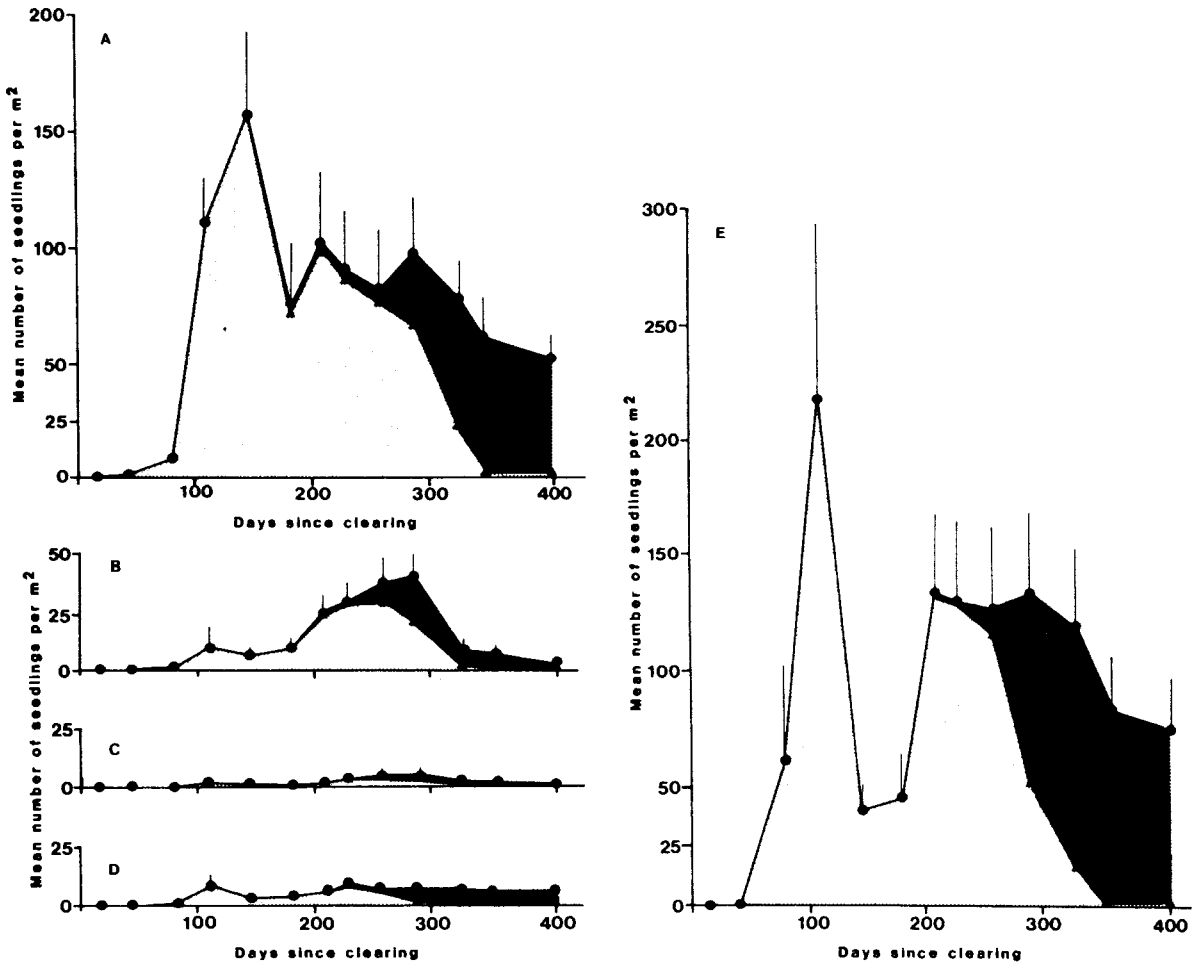

Fig. 3. *Acacia cyclops* seedling emergence and survival following different stand clearing treatments. Total seedling (●—●) and juvenile seedling (<8-week-old) counts (▲—▲) are presented with half standard-error bars ($n=20$ quadrats of 0.25-m^2). The dark shading represents phyllode-bearing seedlings, indicative of survival; and the light shading represents juveniles, indicative of emergence: (A) 'fell and pile', clear area; (B) 'fell, pile and burn' clear area; (C) 'fell, pile and burn', burnt piles; (D) 'burn standing'; (E) 'fell and burn'.

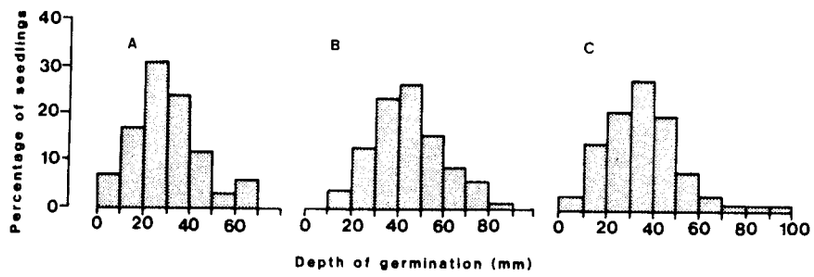

Fig. 4. Depth of *Acacia cyclops* seed germination (mm) following different stand clearing treatments ($n = 105$–120 seedlings: (A) 'fell and pile', clear area; (B) 'burn standing'; (C) 'fell and burn'.

TABLE 4

Effect of different clearing treatments on *Acacia cyclops* seed density (mean number of seeds $m^{-2} \pm$ SE, $n = 50$ cores) 1 year after clearing

	Fell and pile		Fell, pile and burn		Burn standing	Fell and burn
	Clear area	Under slash	Burnt pile	Clear area		
Before clearing	2832 ± 402^{abc}		6774 ± 1019^{a}		7792 ± 666^{bd}	4441 ± 667^{cd}
After clearing						
Plot 1	469 ± 173	224 ± 71	0 ± 0	10 ± 10	0 ± 0	71 ± 46
Plot 2	10 ± 10	41 ± 20	31 ± 20	20 ± 15	31 ± 15	591 ± 132
Plot 3	1192 ± 194	367 ± 565	0 ± 0	132 ± 657	10 ± 10	183 ± 489
Mean reduction (%)	80.3	92.6	99.9	99.2	99.8	93.7

[abcd]Matched pairs are significantly different.

burning versus non-burning treatments indicated that burning was more effective in reducing seed density in the soil (U-test, $P < 0.05$). However, the 'fell and burn' treatment was significantly less effective than the other burning treatments (U-test, $P < 0.05$) and no more effective than the non-burning treatment (U-test, $P > 0.45$). In the non-burning treatment, seed reduction under slash piles was no different from that in clear areas (U-test, $P > 0.3$).

Seeds were distributed from the litter layer to 200-mm depth in the soil prior to clearing, with the litter layer and upper 40 mm of soil containing 95.7% of the seed bank (Fig. 5). After clearing, most seeds in the upper strata were lost, particularly in burning treatments (Fig. 5).

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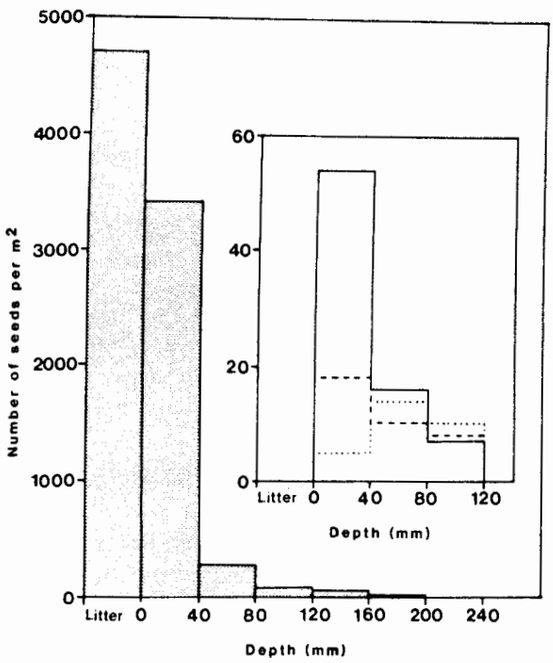

Fig. 5. Vertical distribution of *Acacia cyclops* seeds in the soil before clearing (no. m^{-2}). Inset, Vertical distributions of seeds remaining 1 year after clearing: 'fell and pile', clear area (—); 'burn standing' (- - -); and 'fell and burn' (.....).

DISCUSSION

Acacia cyclops seeds were not stimulated to germinate by fire, in contrast to the marked response of many other Australian *Acacia* species (Auld, 1986; Pieterse and Cairns, 1986). This corroborates the findings of Jeffery et al. (1988), and suggests that *A. cyclops* is not well adapted to fire. The ability of *A. cyclops* to invade fire-adapted fynbos communities must rather relate to its copious production of viable seeds (Milton and Hall, 1981), dispersal by birds (Glyphis et al., 1981) and enhanced germination following disturbance (Gill, 1985).

Despite structural uniformity in the *A. cyclops* stand, soil seed density was heterogeneous among blocks prior to clearing. This may reflect spatial and temporal variation in seed production, germination or decay, rather than inadequate sampling intensity, as standard errors were below 15% of the means (Thompson, 1986). Seed densities were generally higher than in stands of *A. cyclops* sampled elsewhere by Milton and Hall (1981).

The lowest seed-bank reduction of 80% 1 year after clearing exceeds the mean annual decay rate of annual weed seeds in undisturbed and cultivated soils by about 70% and 50%, respectively (Roberts and Feast, 1973), and is

higher than previously recorded for *A. cyclops* 1 year post-clearing (Holmes et al., 1987), possibly owing to the seed population being concentrated near the soil surface at this site. The predictions of a large decrease in *A. cyclops* seed density following all clearing treatments, and the superiority of burning over non-burning treatments (Holmes et al., 1987) are both upheld.

The 'fell and burn' was the least effective burning treatment, and conferred no advantage over felling alone. However, the percentage reduction recorded here was similar to that for an alien *A. longifolia* seed bank following a 'fell and burn' treatment (Pieterse and Cairns, 1986). The greater seedling emergence and smaller median depth of germination than in the 'burn standing' treatment are further evidence that fewer seeds were killed by fire in the 'fell and burn' treatment. The low levels of seedling emergence in the other burning treatments suggest that few seeds survived fire. The 'burn standing' treatment was therefore more severe in its effects than the 'fell and burn' treatment, suggesting some correlation between fire intensity and amount of heat transfer below ground.

In contrast to a previous study (Holmes et al., 1987), where seed banks declined more in areas cleared of *A. cyclops* than under slash piles, this study revealed no difference. The cumulative effect of the higher temperatures experienced at a bare soil surface (Kruger and Bigalke, 1984), may stimulate *A. cyclops* germination (Gill, 1985). At Walker Bay, increased germination in clear areas might have been offset by increased rotting and granivory in the moister conditions and protective cover provided by slash.

Seedling emergence is enhanced under moist conditions, but so is mortality, indicating that pathogens may also be favoured under moist conditions. As few seedlings survived the first 9 months after clearing, follow-up control (i.e. herbiciding or hand-weeding) should be delayed for at least 1 year after the first germination flush. Exposure of the soil surface (i.e. disturbance) is not an essential stimulus for germination, since seedlings emerged under a closed *Acacia* canopy. Seedling emergence accounted for only 16% of seed-bank reduction following felling, therefore predation and rotting must largely account for the difference. Using fresh *A. cyclops* seeds from Walker Bay, Jeffery et al. (1988) found that, after 60 days, 32% of seeds had germinated spontaneously. Since seed-bank viability was high (Holmes et al., 1987), it is likely that a large proportion of seeds germinated in the field but died before being recorded as seedlings, either as a result of pathogenic attack on imbibed and germinating seeds or erosion of newly emerged seedlings exposed to surface sand disturbance. Thus most losses to the *A. cyclops* seed pool occur between seed dissemination and seedling emergence, in common with many other species (Fenner, 1987).

Acacia cyclops does not produce the long-lived seed bank reported for other *Acacia* species (Cavanagh, 1980). Its seed bank has characteristics intermediate between those of persistent and transient seed banks, with a relatively

small proportion of seeds surving the first year, and thus most closely resembles the 'Type-III' persistent seed bank model of Thompson and Grime (1979). The argument that hardseededness in *A. cyclops* may have been strongly selected for in South Africa (Kruger et al., 1986) is not upheld in this study. Being a species associated with disturbance and erosion cycles in its native habitats (Gill, 1985) and being ornithochorous (O'Dowd and Gill, 1986), it may not be advantageous for *A. cyclops* to invest in primarily persistent seed banks. Its apparent hardseededness may be an adaptation to prevent damage by dispersal agents rather than one to enhance dormancy in the soil.

In conclusion, burning is not necessary to produce a rapid seed-bank decline in *A. cyclops*. Since high fire intensities have been shown to kill indigenous sprouting species (Richardson and van Wilgen, 1986), a non-burning treatment may be more appropriate where some indigenous vegetation survives under the *Acacia* canopy. However, the persistence of a few dormant seeds of this weed may cause future management problems. A successful 'burn standing' treatment would result in significantly fewer seeds remaining than after felling alone, and would greatly reduce the costs of clearing dense stands.

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Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa

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The effect of dry heat on the percentage germination, germination rate and lethal temperatures of selected legume species was investigated by exposing seeds to different intensities and durations of heat. Two alien invasive legumes (*Acacia saligna* and *A. cyclops*) and two indigenous legume species: *Podalyria calyptrata*, which is a fynbos species, and *Virgilia oroboides*, a forest precursor, were tested. Results were compared to predictions based on published accounts of the species' ecology. *Acacia saligna* and *P. calyptrata* fitted predictions: high percentage germination, fast germination rates and a tolerance to high temperatures; with *A. saligna* outperforming *P. calyptrata* in the latter two responses. Both *A. cyclops* and *V. oroboides* did not conform to predictions: dry heat had little positive effect on germination, and in *A. cyclops* it had a negative effect.

Die effek van droë hitte op die ontkiemingspersentasie en ontkiemingstempo sowel as die effek van dodelike temperature op geselekteerde peulplantspesies is ondersoek deur die temperature sowel as die blootstellingstyd te varieer. Twee uitheemse indringerpeulplante (*Acacia saligna* en *A. cyclops*) en twee inheemse peulplantspesies: *Podalyria calyptrata*, wat 'n fynbosspesie is en *Virgilia oroboides*, 'n woudpionier, is ondersoek. Die resultate is vergelyk met voorspellings wat gebaseer is op gepubliseerde verslae van die spesies se ekologie. *Acacia saligna* en *Podalyria calyptrata* stem ooreen met die voorspellings wat gemaak is: hoë ontkiemingspersentasie, hoë ontkiemingstempo en 'n toleransie vir hoë temperature; *Acacia saligna* oortref *Podalyria calyptrata* wat laasgenoemde twee aspekte betref. *Acacia cyclops* sowel as *Virgilia oroboides* wyk af van voorspellings wat gemaak is: droë hitte het 'n klein positiewe effek op ontkieming en by *Acacia cyclops* was die effek negatief.

Keywords: *Acacia*, dormancy, invader, lethal temperature, weed control

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Introduction

In South Africa *Acacia cyclops* A. Cunn. ex G. Don. and *A. saligna* (Labill.) Wendl. are ranked among the most important invasive species in the Cape flora according to the extent of their current infestation (Macdonald & Jarman 1984). These *Acacia* species are small leguminous trees or shrubs which produce prolific quantities of hard-coated, water-impermeable seeds (Milton & Hall 1981). Hard coats permit extended seed life, so that seeds are distributed in both time and space (Rolston 1978), posing a major obstacle to the successful control of these invasive species. Germination occurs after the testa is softened or damaged, allowing imbibition (Cavanagh 1980). It appears from the literature that dormancy of water-impermeable seeds may be broken by hot water, dry heat, freezing, organic solvents, acid scarification, mechanical scarification and microwave energy (Pieterse & Cairns 1986a). Fire plays a major role in controlling the Cape fynbos flora, and *Acacia* species tend to become dominant after fire (Cavanagh 1980). It has been shown that under natural conditions heat from a fire may break *Acacia* seed dormancy, resulting in germination (Jones 1963; Pieterse & Cairns 1986b), but with the exception of *A. cyclops* (Jones 1963), no direct effects of dry heat treatment have been undertaken on these species to date.

In this paper we compare the effect of dry heat on seed germination of these two alien species and two indigenous legume species [*Podalyria calyptrata* Willd., and *Virgilia oroboides* (Berg.) T.M. Salter], to ascertain whether germination responses comply with the known ecological behaviour of the species.

Acacia saligna occurs principally in dry sclerophyll forest or temperate woodlands in Australia (Hall & Turnbull 1976): a fire-prone and highly flammable plant assemblage, which burns at 10-year intervals (Christensen *et al.* 1981). In South Africa, *A. saligna* occurs on a wide variety of substrata wherever permanently moist sites are available, forming dense thickets (Milton & Hall 1981). Since *A. saligna* is a successful invader of fynbos, germinating in dense mats following fires [up to 300 seedlings per square metre, (Milton & Siegfried 1981)], we expect that its seed will be stimulated to germinate by heat. Furthermore, we predict that its seed will exhibit a high heat tolerance, because the fuel biomass of *A. saligna* thickets exceeds that of fynbos (Milton & Siegfried 1981), resulting in much hotter fires under extreme weather conditions (van Wilgen & Richardson 1985). Since few seedlings appear to be able to establish in mature stands during interfire periods, we also predict that all viable heat-treated seeds would germinate as soon as suitable conditions prevail.

By contrast, *A. cyclops* is commonly associated with human disturbance and, as a prominent plant in coastal dune assemblages, is rarely subjected to fire in Australia (Gill 1985). Although its seed germination is not dependent on fire in Australia, seeds from South African populations are reported to be harder than most in Australia, suggesting that seed responses to heat may differ between the two continents (Gill & Neser 1984). Although dispersed by birds (Glyphis *et al.* 1981), *Acacia cyclops* germinates extensively after fire in South Africa (Milton & Hall 1981), and responds well to 'dry' and 'wet' heat treatments (Jones 1963). This may be due to either a selection for hardseededness in South Africa, or an initial introduction of a hardseeded ecotype into South Africa (Gill 1985).

Podalyria calyptrata is an indigenous fynbos species, occurring in kloofs and moist hillsides (Jackson 1982). Since fire is an important process in the regeneration of fynbos vegetation (Kruger 1982), we predict that seed of this species will be stimulated by heat to germinate, and exhibit a moderate heat tolerance and a rapid germination rate, as in *A. saligna*.

Virgilia oroboides is a short-lived leguminous tree which occurs on the forest/fynbos margin, as a forest precurser (Jackson 1982). It produces large crops of dormant seed, which may survive in the soil for longer than 30 years, and which germinate extensively after fires (Phillips 1926). Since it parallels the forest precursor role of many *Acacia* species in Australia (Milton & Hall 1981), we expect that its seed germination will be stimulated by heat, as predicted for *A. saligna*.

Methods

Fresh *Acacia* seeds were collected at Walker Bay (34°03′S, 19°24′E) (*A. cyclops*) and Silvermine (34°05′S, 18°27′E) (*A. saligna*). Seeds of *P. calyptrata* and *V. oroboides* were obtained from the Kirstenbosch Botanical Gardens (33°59′S, 18°26′E).

Seeds were treated with dry heat, in preheated ovens, at a range of different temperatures [60, 80, 100, 150 and 215 (± 5) °C], each with a range of durations (1; 2,5; 5; 10; 30 and 60 mins). For each treatment four replicates of 25 seeds each were tested per species (cf. Pieterse & Cairns 1986a). Seeds were allowed to cool and placed in 9-mm sterile, plastic petri-dishes, containing filter paper moistened with 6 ml of benomyl solution [0,022% (m/v) active ingredient] (cf. Clemens *et al.* 1977). Seeds were germinated in a controlled environment of 12 hours light at 25°C alternating with 12 hours darkness at 20°C. Germinated seeds [those with radicles extending 1 – 2 mm beyond the seed coat (Pieterse & Cairns 1986a)] were counted every two days for 30 days and removed. Because *A. cyclops* exhibited a very low germination rate, counts were continued to 60 days, when the experiment was terminated.

For each species, a control (viz. no heat treatment) and a viability trial [seeds manually chipped at the micropylar end to ensure a maximum germination rate (McDowell & Moll 1981)] were conducted as outlined above.

Table 1 The effects of different temperature and duration of temperature treatments on the percentage germination of two alien invader species (*Acacia cyclops* and *A. saligna*) and two indigenous legumes (*Virgilia oroboides* and *Podalyria calyptrata*). For each treatment four replicates, each of 25 seeds, were used

Temperature (°C)	Temperature duration (min)	Percentage germination ($\bar{X}$ ± *SD*, *n* = 4 × 25)				
		A. saligna	*V. oroboides*	*P. calyptrata*	*A. cyclops* (30 days)	*A. cyclops* (60 days)
Control		3 ± 3,8[a]	16 ± 12,6[a]	9 ± 5,0[a]	4 ± 3,3[a]	32 ± 9,8[a]
Viability		98 ± 2,3[b]	89 ± 2,0[b]	85 ± 10,0[b]	100 ± 0,0[b]	100 ± 0,0[b]
60	1	0 [a]	8 ± 3,3[a]	72 ± 5,6[ab]	3 ± 3,8[a]	25 ± 3,8[a]
	2,5	11 ± 2,0[ab]	11 ± 10,0[a]	76 ± 0,0[b]	3 ± 3,8[a]	29 ± 21,0[a]
	5	12 ± 6,3[ab]	18 ± 2,3[a]	92 ± 8,6[b]	3 ± 3,8[a]	39 ± 19,2[a]
	10	21 ± 8,2[ab]	12 ± 5,6[a]	84 ± 10,8[b]	3 ± 2,0[a]	35 ± 10,0[a]
	30	37 ± 14,0[ab]	9 ± 6,0[a]	87 ± 8,2[b]	4 ± 4,6[a]	25 ± 2,0[a]
	60	29 ± 2,0[ab]	6 ± 8,9[a]	84 ± 10,8[b]	5 ± 5,0[a]	16 ± 3,3[ac]
80	1	72 ± 3,3[ab]	21 ± 12,0[a]	85 ± 16,4[b]	4 ± 5,6[a]	38 ± 26,4[a]
	2,5	31 ± 10,5[ab]	8 ± 3,3[a]	88 ± 10,3[b]	0 [a]	14 ± 25,4[a]
	5	62 ± 6,9[ab]	23 ± 2,0[a]	90 ± 12,4[b]	3 ± 2,0[a]	3 ± 2,3[ac]
	10	60 ± 4,6[ab]	21 ± 10,5[a]	87 ± 16,1[b]	1 ± 2,0[a]	23 ± 8,9[a]
	30	81 ± 10,0[ab]	35 ± 11,0[ab]	66 ± 9,5[ab]	1 ± 2,0[a]	18 ± 20,8[a]
	60	69 ± 7,6[ab]	34 ± 10,6[ab]	49 ± 20,0[ab]	0	16 ± 13,1[a]
100	1	52 ± 18,8[ab]	7 ± 8,2[a]	93 ± 6,8[b]	2 ± 2,3[a]	16 ± 10,3[a]
	2,5	30 ± 5,2[ab]	11 ± 5,0[a]	84 ± 8,0[b]	0	14 ± 13,2[a]
	5	26 ± 8,0[ab]	9 ± 3,8[a]	83 ± 12,0[b]	1 ± 2,0[a]	9 ± 11,3[ac]
	10	67 ± 13,2[ab]	11 ± 4,0[a]	91 ± 12,4[b]	1 ± 2,0[a]	11 ± 13,6[ac]
	30	88 ± 6,0[ab]	0	0	0	2 ± 4,0[ac]
	60	23 ± 21,3[a]	0	0	0	0
150	1	70 ± 8,0[ab]	31 ± 14,4[a]	0	1 ± 2,0[a]	30 ± 17,4[a]
	2,5	88 ± 5,2[ab]	27 ± 8,2[a]	5 ± 6,0[a]	0	24 ± 13,8[a]
	5	6 ± 9,5[a]	0	0	0	1 ± 2,0[ac]
	10	3 ± 3,8[a]	0	0	0	0
	30	0	0	0	0	0
	60	0	0	0	0	0
215	1	61 ± 26,4[ab]	20 ± 17,0[a]	0	0	14 ± 11,6[ac]
	2,5	0	0	0	0	1 ± 2,0[ac]
	5	0	0	0	0	0
	10	0	0	0	0	0
	30	0	0	0	0	0
	60	0	0	0	0	0

[a]Significantly lower than the viability ($P < 0,05$)
[b]Significantly higher than the control ($P < 0,05$)
[c]Significantly different from the control ($P < 0,05$) (*A. cyclops* only)

The proportion of seeds that had germinated was expressed as a mean percentage, and compared using a randomization test for two independent samples (Siegel 1956). The average germination rate (in days) was calculated as:

$$\frac{\Sigma\,(gt)}{\Sigma\,(g)}$$

where g is the number of seeds germinating on any one day, and t is the number of days between initiation of the test and the last seed germinating (Jones 1963). Lag phase was calculated as the time taken for 10% of the germinated seed to germinate (Clemens *et al.* 1977). The duration of germination was taken to be the time taken for 90% of the total germinated seed to germinate. A lethal temperature/duration for seeds was arbitrarily defined as those treatments in which the average number of seeds germinating was both half of the control value and significantly different ($P < 0,05$), to that of the control (i.e. approximating an LD_{50}).

Results

Both *P. calyptrata* and *V. oroboides* seed viabilities were significantly lower ($P < 0,05$) than those of the two *Acacia* species (Table 1), with no significant differences in seed viability within the two groups. Percentage germination of the *P. calyptrata* and *V. oroboides* control treatments (9 and 16%, respectively) were significantly higher ($P < 0,05$) than that of *A. saligna* (3%). There were no other significant differences in percentage germination between control treatments. For all species, seed germination in the control treatment was significantly lower ($P < 0,05$) than in the viability treatment.

All temperature/duration treatments in *V. oroboides* resulted in significantly fewer ($P < 0,05$) seeds germinating than in the viability treatment (Table 1). Seed germination was only significantly enhanced ($P < 0,05$) relative to the control at 80°C for 30 and 60 min. In *P. calyptrata* seed germination was significantly enhanced ($P < 0,05$) relative to the control, in all treatments below lethal temperature/duration (Table 1); germination was significantly lower ($P < 0,05$) than that of the viability treatment in only three treatments below the lethal temperature/duration (Table 1). Peak germination of *V. oroboides* and *P. calyptrata* occurred at 60°C for a duration of 10 min, but at 80°C peaked at 5 min for *P. calyptrata* and at 30 min for *V. oroboides*, the latter species

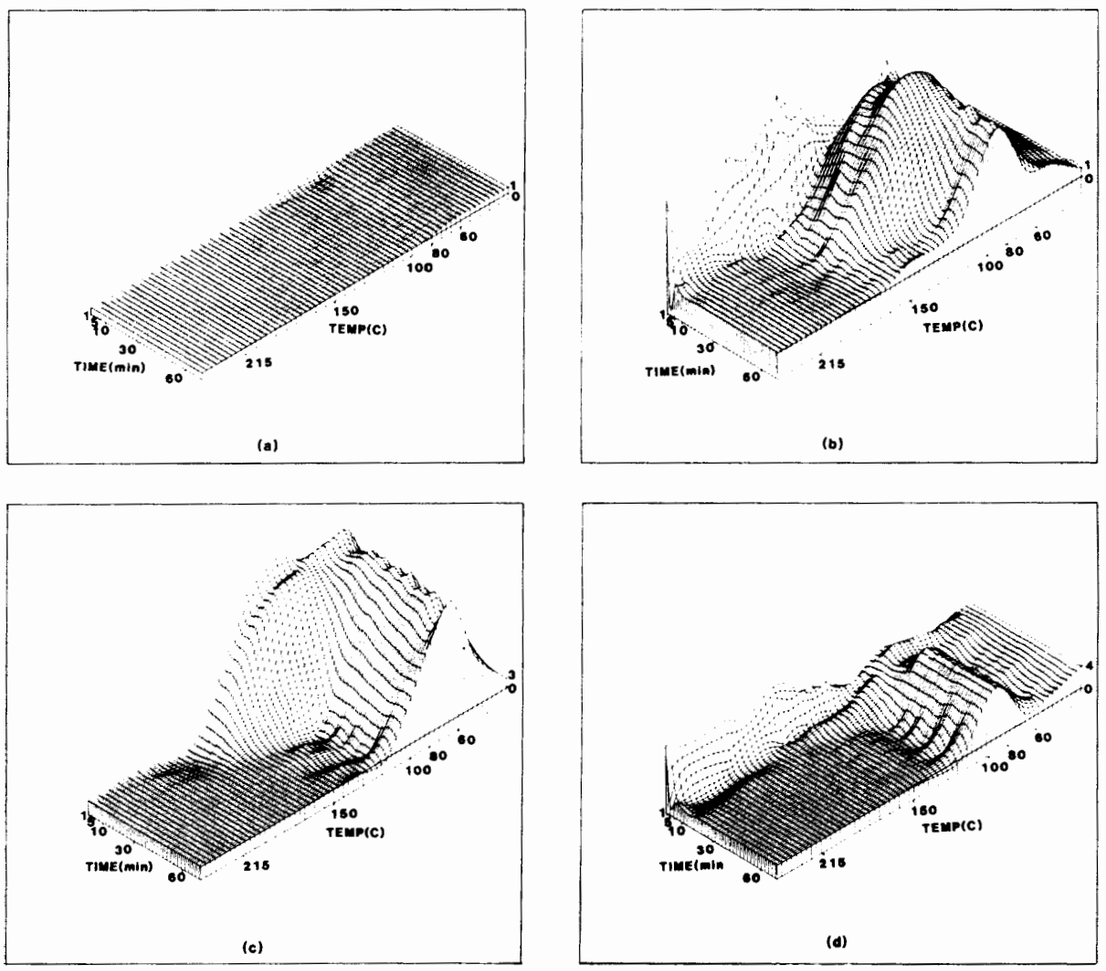

Figure 1 Average and peak germination of seeds 30 days after treatment (vertical axis) with combinations of different temperatures (TEMP) and durations (TIME): (a) *Acacia cyclops*; (b) *A. saligna*; (c) *Podalyria calyptrata*; and (d) *Virgilia oroboides*.

showing no clear peak below lethal durations at 100°C (Figure 1).

Seed germination in *A. saligna* was significantly enhanced (*t*-test, $P < 0,05$) relative to the control in most non-lethal treatments: exceptions were the lowest (60°C of 1-min duration) and highest (100°C at 60-min and 150°C at 5- and 10-min durations) non-lethal treatments (Table 1). In all temperature/duration treatments, significantly fewer seeds germinated than were viable ($P < 0,05$). Peak germination occurred at 30-min duration for temperatures below 150°C, but shifted to short-duration treatments (< 2,5 min) above 100°C (Figure 1).

Very little germination of *A. cyclops* seeds occurred during the first 30 days (Table 1). While no treatments displayed significantly enhanced germination relative to the control, only a very small proportion of the viable seeds had germinated by 30 days. At 60 days, 32% of the viable seeds had germinated in the control treatment. In many of the higher temperature/duration treatments average germination was significantly lower than the control (Table 1). Standard deviations were higher than those in the other species. At 60 days average germination peaked at a temperature of 60°C at 5-min duration, whereas at higher temperatures germination peaked at the shortest time durations (Figure 1).

Average germination rates were negatively correlated with percentage germination in *A. saligna* ($r = -0,43$, $P < 0,05$) and *P. calyptrata* ($r = -0,47$, $P < 0,05$), but no significant correlation was found in either *A. cyclops* or *V. oroboides*. Germination rates of *A. saligna* were much faster than those of the other three species, whilst *A. cyclops* had the slowest rate and longest duration of germination (Table 2). Germination rates of *A. saligna* treatments were faster than the control, but there were no clear trends in germination rate with increasing temperature/duration. However at 60°C, time taken to reach 90% germination was greater than at other temperatures. Germination rates of *V. oroboides*, *P. calyptrata* and *A. cyclops* were not different from their respective controls. In *V. oroboides* germination rate tended to be

Table 2 The effects of different temperature and duration of temperature treatments on the germination rates and duration of germination [expressed as days for 10% germination (lag phase), and until 90% of seeds had germinated] of two alien invader species (*Acacia cyclops* and *A. saligna*) and two indigenous legumes (*Virgilia oroboides* and *Podalyria calyptrata*)

Temperature (°C)	Temperature duration (min)	Rate and duration of germination [No. days/seed (10% seeds, 90% of seeds)]							
		A. saligna		*V. oroboides*		*P. calyptrata*		*A. cyclops*	
Control		16,0	(6; > 30)	14,1	(6;22)	14,1	(8;22)	24,3	(14; > 30)
Viability		2,1	(2; 8)	4,6	(4;13)	5,3	(4; 8)	3,9	(2;6)
60	1	–		12,9	(6;22)	13,5	(6;20)	29,0	(28; > 30)
	2,5	8,2	(4;12)	7,6	(4;16)	13,1	(6;18)	20,0	(12; > 30)
	5	11,4	(4;22)	11,9	(6;27)	12,6	(6;17)	25,0	(19; > 30)
	10	7,9	(4;20)	7,9	(4;15)	13,9	(9;20)	17,3	(12; > 30)
	30	6.0	(4;10)	11,8	(4;23)	13,9	(9;20)	23,3	(21; > 30)
	60	5,7	(4; 7)	8,5	(4;16)	14,3	(9;19)	21,0	(16; > 30)
80	1	4,0	(2; 6)	14,1	(2; > 30)	15,6	(12;21)	27,3	(19; > 30)
	2,5	7,6	(2;21)	15,6	(2;25)	13,4	(10;16)	–	
	5	5,5	(2; 7)	15,6	(10; > 30)	14,2	(8;18)	26,0	(24; > 30)
	10	5,6	(2; 8)	13,7	(8;22)	14,2	(8;21)	24,0	(24; > 30)
	30	5,8	(2; 7)	15,5	(10;22)	17,0	(10;22)	28,0	(29; > 30)
	60	6,8	(2; 8)	13,2	(10;17)	16,8	(12;21)	–	
100	1	4,5	(4; 5)	10,7	(4;16)	14,2	(8;21)	27,0	(25; > 30)
	2,5	4,8	(4; 6)	11,1	(4;22)	12,9	(8,20)	–	
	5	4,7	(4; 6)	16,0	(4;26)	12,5	(8;16)	27,0	(27; > 30)
	10	5,8	(4; 7)	20,0	(11;25)	16,6	(11;21)	29,0	(29; > 30)
	30	7,3	(6; 8)	–		–		–	
	60	9,9	(6;12)	–		–		–	
150	1	6,5	(4; 7)	12,3	(8;18)	–		25,0	(25; > 30)
	2,5	5,9	(4; 7)	14,3	(11;19)	11,0	(6;15)	–	
	5	8,0	(8; 8)	–		–		–	
	10	7,3	(6; 8)	–		–		–	
	30	–		–		–		–	
	60	–		–		–		–	
215	1	8,1	(4;11)	13,2	(9;21)	–		–	
	2,5	–		–		–		–	
	5	–		–		–		–	
	10	–		–		–		–	
	30	–		–		–		–	
	60	–		–		–		–	

slowest at 80°C, whilst in *P. calyptrata* there was a tendency for slower germination rates at longer temperature durations. After 30 days no clear trend was evident in *A. cyclops* germination rates.

Lethal temperature/durations for seeds of *V. oroboides* and *A. cyclops* were 100°C for durations of 30 min and longer, 150°C for longer than 2,5 min and 215°C for longer than 1 min (Figure 2). In *P. calyptrata* lethal temperature/durations were 100°C for 30 min and longer, and even brief exposures at 150°C and above killed the seeds. Lethal temperature/durations for *A. saligna* were 150°C for longer than 5 min and 215°C for longer than one min.

Discussion

Our understanding of the reproductive biology of alien invasive species has increased greatly in recent years (Milton & Hall 1981). Whereas seed biology has been recognized as a key factor in the successful establishment of invasive acacias, to date little ecological interpretation of laboratory results has taken place in South Africa.

Acacia saligna seeds respond to dry heat treatments as predicted from extrapolations of its ecological behaviour. Percentage germination is high following exposure to dry heat, germination is rapid and there is a marked tolerance to high temperatures. These responses probably preadapted *A. saligna*

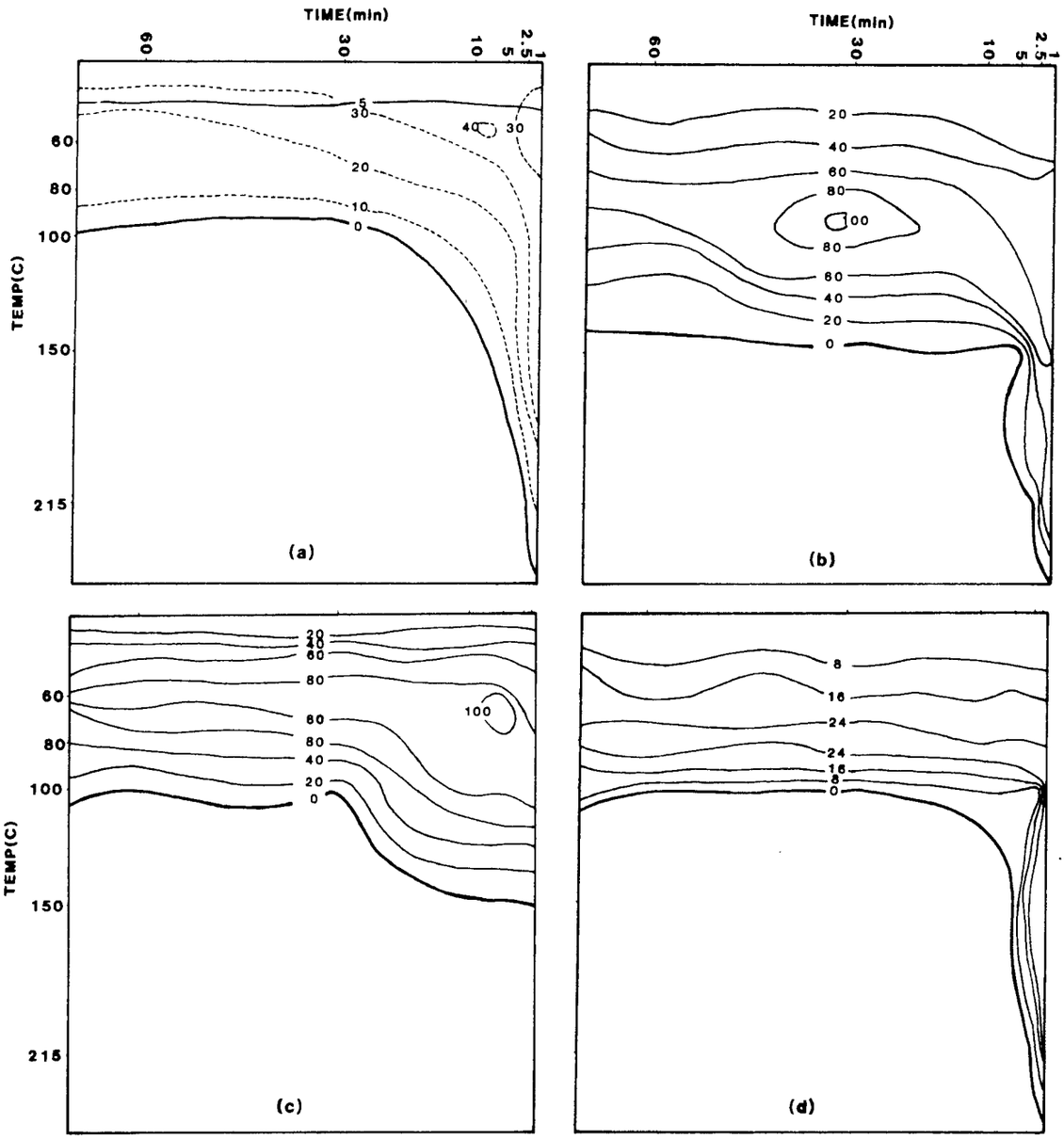

Figure 2 Proportion of seeds germinating for different temperature (TEMP) and duration (TIME) treatments (expressed as a percentage of potentially viable seeds) of seeds 30 days after treatments: (a) *Acacia cyclops* (dotted line = after 60 days); (b) *A. saligna*; (c) *Podalyria calyptrata*; and (d) *Virgilia oroboides*. Lethal temperature/durations are indicated by the 0 isogerm.

to South African fynbos conditions, with the high rate of germination additionally providing a competitive edge over slower-germinating fynbos species. The fact that germination following heat treatment is lower than the viability, suggests that a proportion of the seeds might remain dormant and only germinate after another fire (i.e. distribution in time over fire seasons).

Similarly, *P. calyptrata* also behaves as expected. Percentage germination is high, germination is rapid and it has a moderate tolerance to high temperatures. However, *A. saligna* surpasses *P. calyptrata* in the latter two responses.

Germination of *A. cyclops* and *V. oroboides* seed does not conform to predictions based on their known ecology. Whilst results for *A. cyclops* are difficult to interpret since the experiment did not continue until all the seeds had germinated, at 60 days there were no obvious effects of different dry heat treatments on the proportion of seeds germinating. Whereas this result may have been predicted under Australian conditions where it is a dune colonizer, the result is incongruous with South African conditions where it is reported in the literature to be hard-seeded and adapted to fire (Gill 1985). The spread of *A. cyclops* in South Africa has been aided by transport of seeds in soil used for road-building (pers. obs, cf. Gill 1985) and by bird dispersal, the latter simultaneously scarifying the seeds which improves germinability (Glyphis *et al.* 1981). Milton & Hall (1981) found that *A. cyclops* seeds did not germinate following immersion in hot water, but 87% of viable seeds germinated when given two hot water immersion treatments. Cavanagh (1980) found *Acacia* seeds to be adversely affected by prolonged exposure to moist heat. These results suggest that the intensity of heat may not be as important as the frequency of heat treatments. In Australia prolonged mild heat (60°C) treatments or repeated exposures to alternating mild and cooler temperatures increases *A. cyclops* seed germination relative to controls (Gill 1985). *A. cyclops* seeds may thus respond to moderate, fluctuating soil temperatures, heated by sunlight during the day, in a manner similar to that of Cape Proteaceae with nut-like fruits (Brits 1986). This might allow seed germination in areas of bare soil, such as dunes and quarries, without the need for fire stimulation. The negative effect of high temperatures on seed germination relative to the control, might perhaps be due to a hardening of the testa at high temperatures. This would explain the observed reduction in germination, by means of a possible increase in impermeability of the testa, without implying that embryos may have been adversely affected by moderately high temperature treatments. This does not comply with known mechanisms involving rupture of the lens in hard-seeded legume species (Tran & Cavanagh 1984).

Similarly, germination of *V. oroboides* seeds is poorly stimulated by dry heat treatments, and no relationship exists between the rate of germination and the number of seeds germinating. *Virgilia oroboides* may perhaps parallel *A. cyclops* in requiring a less intensive heat treatment, but one of a cyclical nature, thus allowing it to colonize disturbed areas within forests.

It is therefore possible that two strategies might exist in hard-seeded legume species in the south-western Cape: those species primarily occurring in fire-prone communities with seeds mainly requiring a single high-temperature treatment to break dormancy or stimulate germination; and those species occurring in less fire-prone communities (e.g. dune communities, forest communities, etc.), in which seeds predominantly require a cyclical, less severe heat treatment, such as may occur on exposed soil surfaces, to stimulate germination.

If the above hypothesis is true, the seed biology of *A. cyclops* suggests that it should invade badly disturbed areas (such as quarries, dunes, etc.) more efficiently than *A. saligna*. *Acacia saligna* would however be a more efficient initial colonizer of mature plant assemblages, and should be able to establish itself in areas stabilized by *A. cyclops*.

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(b) **Pre-dispersal seed predation**

Paper 5. Holmes P.M., Dennill G.B. & Moll E.J. 1987. Effects of feeding by native alydid insects on the seed viability of an alien invasive weed, *Acacia cyclops*. S. Afr. J. Sci. 83:580-581.

Paper 6. Holmes P.M. & Rebelo A.G. 1988. The occurrence of seed-feeding *Zulubius acaciaphagus* (Hemiptera, Alydidae) and its effects on *Acacia cyclops* seed germination and seed banks in South Africa. S. Afr. J. Bot. 54:319-324.

Effects of feeding by native alydid insects on the seed viability of an alien invasive weed, *Acacia cyclops*

P.M. Holmes, G.B. Dennill* and E.J. Moll

Acacia cyclops A. Cunn. ex G. Don was introduced to South Africa from Australia *c.* 1835.[1] During the late 19th and early 20th centuries, it was widely planted for dune stabilization, shelter-belts and hedges in the southern and south-western Cape.[2] *Acacia cyclops* was soon noted for its invasiveness in sandy or coastal habitats[3] and recently (1984) was rated the third most important invasive plant in the fynbos biome.[4] In this note the effect of hemipteran feeding on *A. cyclops* seeds in South Africa is examined. Feeding significantly reduced seed viability and evidence is presented, indicating that this feeding may substantially reduce seed density in the soil. These insects are probably indigenous, and we suggest that they have only recently begun to exploit this food source.

The invasiveness of *A. cyclops* in South Africa is largely due to its prolific production of long-lived, hard-coated seeds,[5] which are dispersed into native vegetation by birds[6] and are later stimulated to germinate by fire.[7] In general, these seeds are free from the heavy insect predation observed in Australia[5,8] where a range of hemipteran bugs feed on the developing and mature seeds, both on the trees and on the ground.[9,10] These bugs make minute feeding holes in the testae, causing seeds to imbibe moisture and either germinate or rot.[10] Consequently, large *A. cyclops* seed banks are unknown in Australia.[8] In South Africa, however, most seeds fall directly to the ground and seed banks of up to 5140 seeds m^{-2} have been measured under mature stands.[11] One of the keys to controlling the future spread of this plant is to reduce viable seed production substantially and thus the number of seeds reaching 'safe' sites.[12]

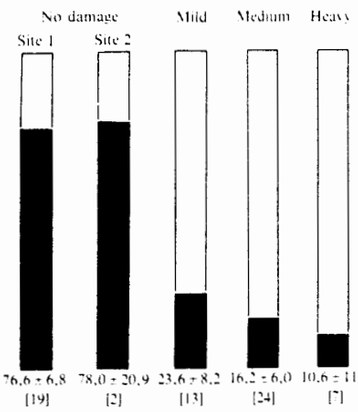

Fig. 1. Mean percentage germination of *Acacia cyclops* seeds fed on at different intensities by alydid bugs. The mean ± 99% confidence limits and the number of replicates, each containing 25 seeds (in square brackets), are given beneath the bars. Undamaged, mild, medium and heavy seed-damage were categorized by having 0, 1 – 5, 5 – 15, and >15 feeding holes visible per seed. Additional seeds were collected from an uninfested area (site 1), because of the small sample of undamaged seeds available at the study area (site 2). Germination was induced by one hot water treatment.[17] Differences in percentage germination between damaged versus undamaged seeds and between mildly versus heavily damaged seeds are highly significant ($P<0,01$, ANOVA).

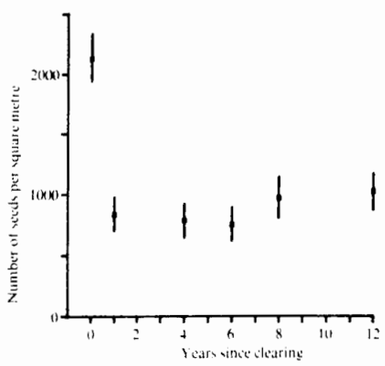

Fig. 2. *A. cyclops* seed density in the soil (mean ± s.e.m., n = 60) in blocks of different ages since felling.

Species from at least four alydine genera have been recorded on both indigenous and exotic acacias in South Africa,[13] with at least one genus (*Zulubius*, Alydidae: Alydinae) present on *A. cyclops*. These *Zulubius* species are considered to be African (currently being described, J.C. Schaffner, personal communication). Since alydines are predators on pods and seeds of leguminous plants,[13] it is probable that the two or more *Zulubius* species feeding on *A. cyclops* are indigenous, having adopted this food source from indigenous plants such as *Acacia karroo*.

Many pests of introduced crop species are recruited from their new habitat and not imported with the plant.[14–16] The number of such crop pest species accumulates rapidly to a maximum which is reached within, at most, a few hundred years, depending on the area of crop under cultivation.[15] Similarly, it may be anticipated that local insect species would colonize *A. cyclops*, which also occurs in large monospecific stands.

Germination trials showed that alydid feeding substantially reduced the viability of *A. cyclops* seeds (Fig. 1). There was a strong negative correlation between feeding intensity (based on counts of feeding holes) and percentage germination ($r=0,84$; $P<0,001$). Mild feeding (1 – 5 holes per seed) alone reduced seed viability to 24%. Because hot water treatment was used to break seed dormancy, a further trial was carried out to confirm that the hot water did not reduce the viability of alydid-damaged seeds. Five replicates each of undamaged and damaged seeds (25 seeds per replicate) were placed in Petri dishes on moist filter paper and incubated in the dark at 16°C. No germination occurred; however, whereas undamaged seeds remained dormant, damaged seeds imbibed moisture and rotted, confirming that alydid feeding was the cause of reduced viability. Earlier studies of cowpeas fed on by hemipterans (Alydidae) also showed decreasing viability with increasing feeding intensity.[18,19]

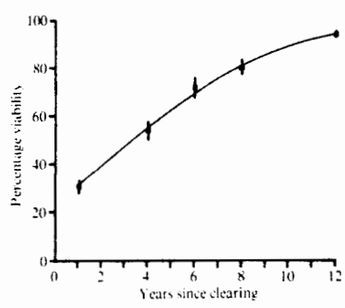

Fig. 3. Percentage viability of soil-stored *A. cyclops* seeds (mean ± s.e.m. of three replicates, each of 50 seeds) from blocks of different ages since felling. A logistic model, $\log [\pi/(1-\pi)] = -1,147 + 0,332t$, where π = probability of a viable seed and t = time (years since felling), was fitted to the data using GLIM[20] and was used to draw the curve. The increase in percentage viability with time after felling is highly significantly ($P<0,0001$, χ^2 test).

In the southern Cape an *A. cyclops* stand, established about 45 years ago, was felled in blocks over a 12-year period and kept clear of *A. cyclops* seedlings. Changes in seed density in the soil since felling were determined in July 1985 by counting seeds from 60 randomly located cores (5 cm diameter by 15 cm deep) extracted in each block. Seed density decreased sharply in the first year after clearing (Fig. 2), with no significant decrease thereafter (*Z*-test, $P>0,05$). Since *A. cyclops* seeds are characteristically hard-coated and long-lived, this initial decline in seed density may be due

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to alydid-damaged seeds imbibing water and rotting in the soil. The persisting seeds, which have not been fed upon, will remain dormant in the soil until their testae are sufficiently scarified. The fact that seed banks in blocks recently cleared are not significantly larger than those cleared 8 and 12 years previously, despite additional years of seed fall, suggests that the intensity of seed predation on *A. cyclops* is increasing.

As alydid-damaged seeds imbibe moisture and rot in the leaf litter and soil, the proportion of viable seeds remaining in the seed bank increases with time. We tested the soil-stored seeds collected from the blocks cleared at different times for percentage viability. Seeds were chipped at their micropylar end to break seed coat-imposed dormancy.[11] Three replicates of seeds (50 seeds/replicate) were placed in Petri dishes on moist filter paper and incubated at 20°C. A highly significant increase in percentage viability occurred with time after clearing, confirming that damaged seeds are eliminated first, leaving an increasing proportion of viable seeds in the seed bank (Fig. 3).

From these results we suggest that the beginning of a 'pest' species accumulation on *A. cyclops* is being witnessed. An observed effect of this is a reduced output of viable seeds with a possible corresponding reduction in the invasive potential of the plant. Although the problem of extant seeds banks remains, the accumulation of large *A. cyclops* seed banks may become a feature of the pest in South Africa. However, successful control of weed species by indigenous insects is unusual[21] and does not obviate the need for a comprehensive biological weed control programme.

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The occurrence of seed-feeding *Zulubius acaciaphagus* (Hemiptera, Alydidae) and its effects on *Acacia cyclops* seed germination and seed banks in South Africa

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Following recent observations of an indigenous hemipteran *Zulubius acaciaphagus* feeding on alien *Acacia cyclops* seeds, we surveyed its occurrence and effects throughout the plant's distributional range. *Zulubius acaciaphagus* occurred at all study sites, but when surveyed was most abundant at the north-western extreme of the plant's distributional range, where the climate is hotter and drier. Intensity of feeding correlated positively with percentage seed rotting and negatively with percentage seed viability, but was not correlated with percentage spontaneous seed germination. Soil-seed density did not relate to alydid density, possibly because feeding intensity was low; mean maximum daily temperature and annual rainfall (or related factors) apparently have a major effect on seed density. Although *Z. acaciaphagus* destroyed up to 84% of the *A. cyclops* seed crop, detailed studies of the alydid's population dynamics are required to assess its potential as a controlling agent of the alien invader.

Na aanleiding van onlangse waarnemings van 'n inheemse halfvlerkige *Zulubius acaciaphagus* wat op uitheemse *Acacia cyclops*-sade voed, is die voorkoms en gevolge daarvan oor die plant se hele verspreidingsgebied ondersoek. *Zulubius acaciaphagus* het in alle studiegebiede voorgekom, maar was tydens die ondersoek die volopste by die noordwestelike grens van die plant se verspreidingsgebied, waar die klimaat warmer en droër is. Die intensiteit van die voeding het positief met die persentasie verrotte saad gekorreleer en negatief met die persentasie saadkiemkragtigheid, maar is nie met die persentasie spontane saadontkieming gekorreleer nie. Die digtheid van saad in die grond hou nie verband met die alydid-digtheid nie, moontlik weens die feit dat die maksimum daaglikse temperatuur en jaarlikse reënval (of verwante faktore) waarskynlik 'n groot invloed op saaddigtheid het. Alhoewel *Z. acaciaphagus* tot 84% van die *A. cyclops*-saad vernietig, word gedetailleerde ondersoeke na die alydid-populasiedinamika benodig om die potensiaal daarvan as beheeragent van die uitheemse indringer te bepaal.

Keywords: *Acacia cyclops*, alydids, distribution, seed bank, seed germination

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Introduction

Acacia cyclops A. Cunn. ex G. Don is a small evergreen tree, introduced into South Africa from Australia in the late 19th century for dune stabilization and shelterbelts (Shaughnessy 1980). It has become one of the most widespread alien invaders in the lowlands of the fynbos biome (Figure 1; Macdonald *et al.* 1985). Its invasive success is thought to be primarily due to a 'preadaptation' to climatic and edaphic conditions in the south-western Cape and to its 'ecological release' from pathogens and predators (Milton 1980). Although its seed production is similar in South Africa and Australia, seed banks are much larger in South Africa (Gill & Neser 1984). These large seed banks are a major obstacle to its successful control (Holmes *et al.* 1987b).

Acacia cyclops is attacked by many seed-feeding insect species in native western Australia, including nine hemipterans (van den Berg 1980). Predation by a single species of hemipteran was found to account for the destruction of 25% of the seed crop (van den Berg, loc cit), and predation may thus explain the low seed banks found in Australia. Unlike chewing insect predators (e.g. Lepidoptera and Coleoptera), which consume whole seeds (Moore 1978), hemipterans puncture seeds (Underhill 1943) and may only kill seeds if the embryo is damaged (Janzen 1976). Hemipteran feeding punctures may break the water-impermeable, seed-coat dormancy (Rolston 1978) of *A. cyclops* seeds (Neser 1984).

Recently, an alydid bug (*Zulubius acaciaphagus* Schaffner, Alydidae: Alydinae) has been observed feeding on the canopy-held seeds of *A. cyclops* in South Africa. Although initial observations of *Z. acaciaphagus* on *A. cyclops* were made in 1975 (Schaffner 1987), it is uncertain when initial colonization of *A. cyclops* by *Z. acaciaphagus* (c.f. Strong 1974) occurred. *Zulubius acaciaphagus* has been shown to markedly decrease the viability of *A. cyclops* seeds, and may possibly reduce the rate of seed accumulation in the soil (Holmes *et al.* 1987a). Little is known about the distribution of *Z. acaciaphagus* and the extent of its attack on *A. cyclops* seeds in South Africa. In this paper we investigate the distribution of alydids on *A. cyclops* and assess the effects alydids have on *A. cyclops* seeds and seed banks.

Field sites and Methods

Studies were made between 27 December 1986 and 10 January 1987 at 16 sites supporting dense (i.e. canopy cover > 90%) stands of mature *A. cyclops* throughout the plant's distributional range (Figure 1). At each site, 10 trees were selected at random to assess alydid presence and seed damage. The proportion of deformed seeds (i.e. those with a shrunken or depressed appearance), which might be the result of alydid feeding on developing seeds, was determined by inspecting 100 seeds in newly dehisced pods on each tree. The number of feeding turrets (c.f. Gill 1985) per seed was recorded for 100 undeformed seeds on each tree. The density of *Z. acaciaphagus* adults and nymphs from each tree was determined as follows: dehisced pods containing seeds were carefully removed from randomly selected branches, placed into plastic bags and sprayed with insecticide. Any *Z. acaciaphagus* present were sorted into adults, large nymphs (> 2 mm long), and small nymphs (< 2 mm long) and expressed as a proportion of seeds collected (112–732 seeds, or *ca.* 50 pods, per tree). Although the overwintering behaviour of alydid adults is not known, mature seeds are available on *A. cyclops* trees for 5 months (Knight 1986) beginning in October, with developing seeds available prior to this (pers. obs). Alydid populations should thus have attained seasonal abundance by the time of this study.

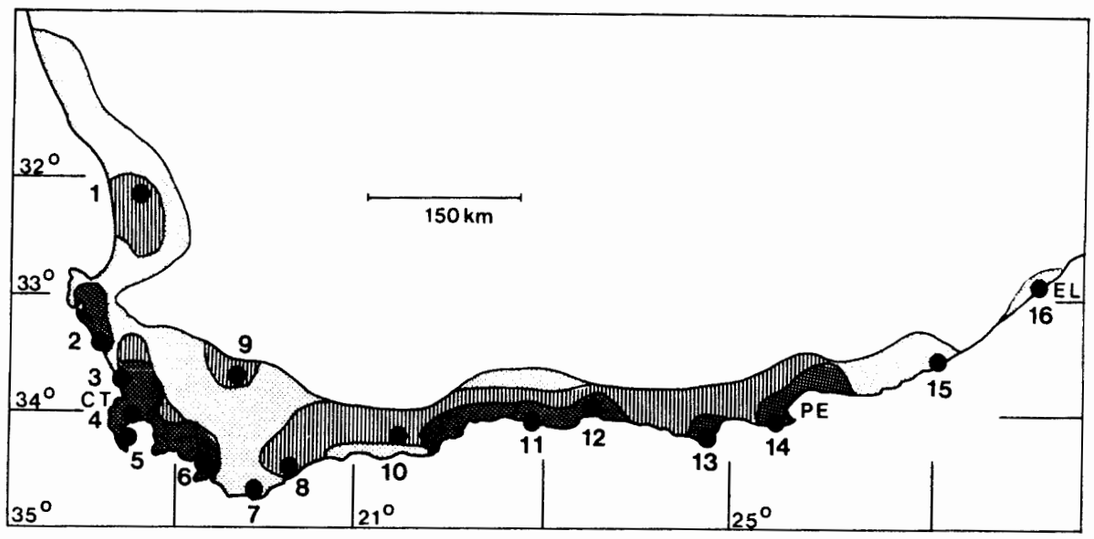

Figure 1 Distribution and infestation density (stippled = scattered plants; striped = moderate; solid = dense) of alien *Acacia cyclops* in South Africa (from Macdonald *et al.* 1985), showing locations of the 16 study sites.

Stand density and demography of *A. cyclops* were estimated at each site by measuring all stem diameters (at 0,1 m above ground) in a 10-m × 10-m plot. Trees were classified into < 3-cm, 3–5-cm, 6–20-cm, and > 20-cm stem diameter categories. Wood biomass was estimated from stem diameters using regression equations from Milton & Siegfried (1981). Density of seeds in the soil was determined by extracting 50 random soil cores (50 mm diameter × 150 mm deep) within the 10-m × 10-m plot.

Germination trials

Undeformed seeds collected from the 10 trees at the 16 sites were tested for percentage spontaneous germination (germination) and percentage decay (rotting) as follows: four replicates of 25 seeds each per tree were placed in 9-mm sterile, plastic petri-dishes, containing filter paper moistened with 6 ml benomyl solution [0,022% (m/v) active ingredient, c.f. Clemens *et al.* 1977]. Seeds were germinated in a controlled environment with a 12-h photoperiod at 25°C alternating with 20°C. Germinated seeds [those with radicals extending 1–2 mm beyong the seed coat (Pieterse & Cairns 1986)] and rotted seeds were counted and removed over a period of 26 days. Remaining seeds were considered to be dormant and were manually chipped at the micropylar end to ensure a maximum germination rate (McDowell & Moll 1981), and incubated for a further 14 days to determine percentage viability (viability).

Soil-stored seeds from 12 sites (seeds from four sites were not tested) were also subjected to germination trials, as described above with four replicates of 25 seeds each per site. In addition, four replicates of 25 seeds classified as deformed were tested for viability.

Data analysis

The importance of selected site factors in determining soil-stored seed and alydid densities, and germination response of fresh seed, was tested by stepwise multiple linear regression analysis (SMLRA, BMDP2R, Dixon 1985) using means from each of the 16 sites. Climatic data were taken from the nearest weather station (Appendix 1). Infestation level of *A. cyclops* at each study area was extracted from Macdonald *et al.* (1985) (Figure 1).

Correlation analysis (BMDP6D, Dixon 1985) was employed to test effects of alydid density and feeding intensity (% seeds with at least one turret) on seed germination response, using data from 10 trees at each site. Clumping of feeding turrets was investigated by Chi-squared testing deviations from the Poisson distribution (Zar 1974). Differences in germination response between fresh and soil-stored seeds were tested by the Mann–Whitney U Test (Siegel 1956).

Results

Zulubius acaciaphagus adults or nymphs were found at 14 of the 16 sites investigated (Figure 2), but all life-cycle stages were sampled only at Klipfontein and East London. However Klipfontein, in the extreme north-west, supported over 100 times the density of any other site. No other *Zulubius* species was collected. There was evidence of alydid feeding at all 16 sites, but only the three north-westerly sites (Klipfontein, Fairvlei and Koeberg) had more than 25% of seeds with feeding turrets (Figure 3). Alydid density was positively correlated with mean maximum daily temperature and negatively correlated with mean annual precipitation (r=0,557, r=−0,506, respectively; $P < 0,05$). Mean maximum daily temperature explained 31% of the inter-site variation in alydid density (Table 1).

At an inter-site level, average germination of fresh seeds was positively correlated with mean average daily temperature (r = 0,501, $P < 0,05$), which accounted for 25% of the variation (Table 1). Seed rotting was positively correlated with alydid large nymphs and small nymphs (r = 0,889 and r = 0,823 respectively, $P < 0,001$), which accounted for 85% of the inter-site variation (Table 1). Alydid density, feeding intensity and site factors such as precipitation and temperature, accounted for 97% of the variation in seed rotting (Table 1). Viability was not correlated with any variable at an inter-site level.

Estimated density of soil-stored seeds ranged from 28 seeds m^{-2} near East London to 11 400 seeds m^{-2} at Arniston (Figure 4). Soil-stored seed density was not correlated with any measure of alydid or plant density, but was negatively correlated with mean maximum daily temperature (r = −0,597, $P < 0,05$). Mean maximum daily temperature and annual precipitation accounted for 50%

of the inter-site variation in seed density (Table 1).

Numbers of *Z. acaciaphagus* adults, large nymphs and small nymphs and their visible effects — percentage deformity and turrets (analysed for 10 trees per site) — were all

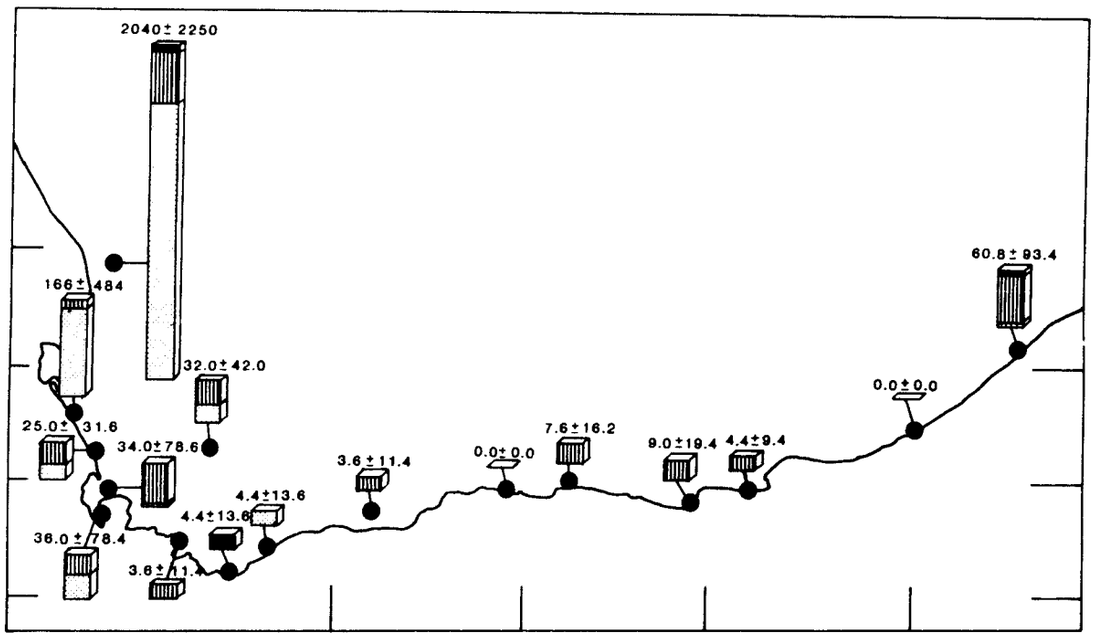

Figure 2 Density of *Zulubius acaciaphagus* adults, large nymphs and small nymphs on *Acacia cyclops* at 16 sites in South Africa (drawn to a square root scale). Stippled = small nymphs; striped = large nymphs; solid = adults; numbers are mean alydids per 10 000 seeds ± *S.D.*, *n* = 10 samples.

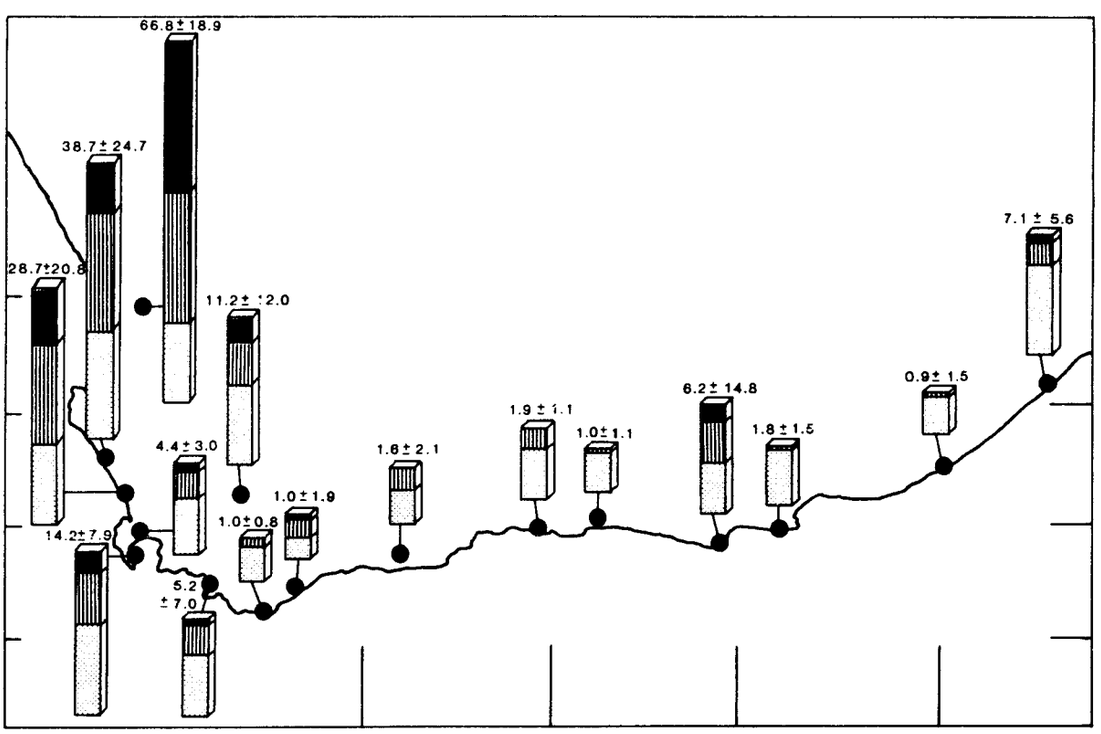

Figure 3 Density of alydid feeding turrets (% seeds with turrets) on *Acacia cyclops* seeds at 16 sites in South Africa (drawn to a square root scale). Stippled = 1 turret per seed; striped = 2–3 turrets per seed; solid = 4 or more turrets per seed; numbers are mean percentage turrets ± *S.D.*, *n* = 10 samples.

significantly correlated among each other (Table 2). The distribution of alydid feeding turrets on seeds at the three sites with the highest feeding intensity was highly clumped (mean = 1,147, *S.D.* = 1,636; $P < 0,05$, Chi-squared test).

Germination of fresh seeds was low (Table 3), and was not correlated with alydid density or feeding intensity (Table 2). Within sites, seed rotting during the first 26 days of the germination trials was positively correlated with alydid density (Table 2). Seed viability showed significant ($P < 0,05$) negative correlations with all measures of alydid density except the density of small nymphs (Table 2). All seeds classified as deformed were non-viable.

Seed germination and viability were significantly lower in fresh seeds than in soil-stored seeds at six and nine of the 12 sites respectively (Table 3). Rotting in the first 26 days was significantly higher in fresh seeds than in soil-stored seeds at eight of the 12 sites (Table 3).

Discussion

There is evidence of *Z. acaciaphagus* throughout the distributional range of *A. cyclops* in South Africa, but it is most abundant in hotter and drier environments. The species shows no relationship to *A. cyclops* density or demography.

Alydids apparently cause an increase in rotting and a decrease in viability of *A. cyclops* seeds. Whilst alydid feeding may break water-impermeable, seed-coat dormancy (Neser 1984) this appears to cause rotting rather than increased germination. Although damage to the embryo may be required to kill a seed (Janzen 1976), any puncture may introduce bacterial and fungal pathogens (Janzen 1971), which may lead to rotting in moist environments. Furthermore, hemipterans can be vectors of fungi (Green & Palmbald 1975). This is supported by the high correlation between seed rotting and alydid density. The correlation

Table 1 Results of stepwise multiple linear regression analysis. Significance levels are $P < 0,1$

Dependent variables							
Soil-seed density		Alydid density		Germination (fresh seeds)		Rotting (fresh seeds)	
Independent variables	r^2	Independent variable	r^2	Independent variable	r^2	Independent variables	r^2
tmax	-0,356	tmax	0,310	tavg	0,251	alln	0,790
pptan	-0,145					alsn	0,057
densl	0,105					turr	0,024
						pptan	0,049
						inflev	0,017
						pptsu	0,013
						def	0,007
						tavg	0,009
						tmax	0,006
Overall regression equation	0,606		0,310		0,251		0,972

Abbreviations are as follows: tmax = mean maximum daily temperature; pptan = annual precipitation; densl = density of stems, diameter < 3 cm; tavg = average daily temperature; alln = large nymphs; alsn = small nymphs; turr = % seeds with turrets; inflev = infestation level; pptsu = summer precipitation; def = % deformed seeds

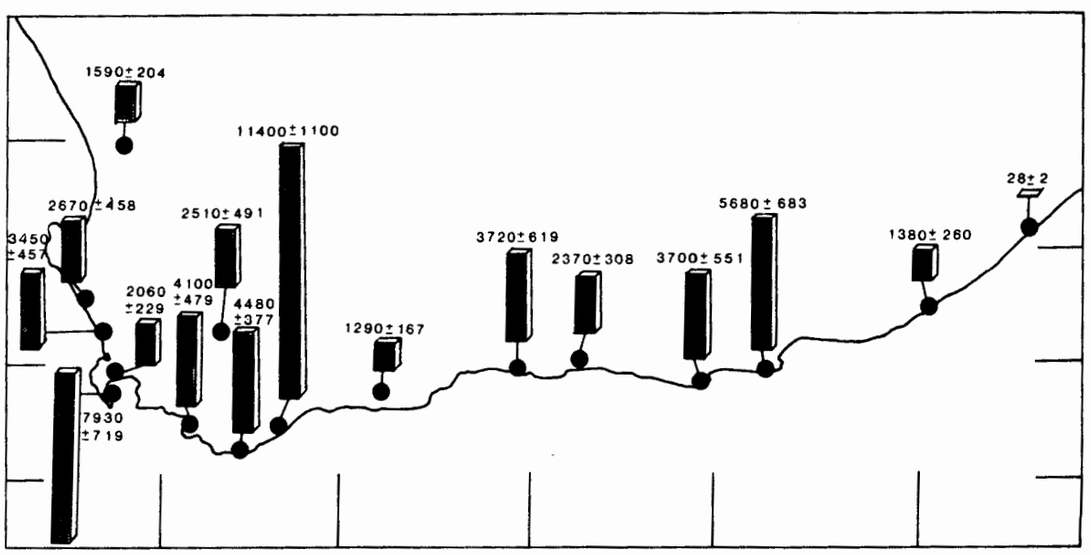

Figure 4 Density of soil-stored *A. cyclops* seeds at 16 sites in South Africa; numbers are mean seeds $m^{-2} \pm S.E.$, $n = 50$ samples.

Table 2 Correlation coefficients among % seed deformity, % seeds with turrets, adults, nymphs > 2 mm, nymphs < 2 mm and seed germination response for 10 trees at 16 sites (n = 159; $^*P < 0{,}05$; $^{**}P < 0{,}01$)

	Rotting 26 days	Viability	Deformity	Turrets	Adults	Nymphs > 2 mm	Nymphs < 2 mm
Germination	0,062	-0,045	-0,040	0,002	-0,041	-0,048	-0,014
Rotting		-0,426**	0,537**	0,564**	0,451**	0,542**	0,296**
Viability			-0,253**	-0,264**	-0,167*	-0,274**	-0,132
Deformity				0,551**	0,474**	0,644**	0,434**
Turrets					0,504**	0,610**	0,511**
Adults						0,749**	0,295**
Nymphs > 2 mm							0,622**

Table 3 Comparison of germination trial results between fresh and soil-stored seeds. Mean % ± *S.D.*, n = 40 for fresh seeds and n = 4 for soil seeds ($^*P < 0{,}05$; $^{**}P < 0{,}01$, Mann–Whitney U Test)

Site	% Germination		% Viability		% Rotting (26 days)	
	Fresh	Soil	Fresh	Soil	Fresh	Soil
1	0,56 ± 0,73	1,00 ± 2,00	45,6 ± 16,7	77,0 ± 9,5**	27,10 ± 17,30**	8,0 ± 3,3
2	0,50 ± 0,71	1,00 ± 2,00	72,2 ± 12,3	92,0 ± 4,6**	7,30 ± 7,69*	0,0 ± 0,0
3	1,30 ± 1,77	1,00 ± 2,00	55,1 ± 23,8	90,0 ± 4,0**	7,40 ± 5,70*	1,0 ± 2,0
4	0,20 ± 0,42	-	62,6 ± 22,9	-	6,60 ± 10,60	-
5	0,40 ± 0,70	-	70,7 ± 16,3	-	5,70 ± 4,27	-
6	0,20 ± 0,42	2,00 ± 4,00	74,8 ± 16,3	99,0 ± 2,0**	2,90 ± 3,76	1,0 ± 2,0
7	0,10 ± 0,32	3,00 ± 3,38	76,2 ± 11,5	85,0 ± 10,5	2,80 ± 2,35	1,0 ± 2,0
8	1,00 ± 1,49	23,00 ± 8,87**	60,9 ± 20,7	88,0 ± 0,0**	0,80 ± 1,14**	0,0 ± 0,0
9	0,60 ± 0,70	4,00 ± 5,66	35,2 ± 23,6	94,0 ± 5,2**	0,80 ± 0,92	4,0 ± 3,3
10	0,40 ± 1,00	23,00 ± 11,02**	88,9 ± 12,4	91,0 ± 8,3	1,30 ± 1,42**	0,0 ± 0,0
11	0,20 ± 0,63	-	89,5 ± 9,5	-	3,30 ± 3,65	-
12	0,30 ± 0,48	66,00 ± 13,3**	67,5 ± 15,6	100,0 ± 0,0**	3,50 ± 1,27**	0,0 ± 0,0
13	0,20 ± 0,42	12,00 ± 8,64**	71,2 ± 18,8	85,0 ± 12,4	8,20 ± 7,96	3,0 ± 2,0
14	1,00 ± 0,94	48,00 ± 8,64**	61,8 ± 18,7	97,0 ± 3,8**	3,90 ± 3,29**	0,0 ± 0,0
15	3,30 ± 3,30	16,00 ± 9,24**	73,6 ± 11,6	86,0 ± 5,2*	7,00 ± 5,75**	0,0 ± 0,0
16	2,30 ± 3,80	-	55,6 ± 15,4	-	16,40 ± 8,73	-

between germination and mean average daily temperature is consistent with Gill's (1985) findings in Australia that percentage germination of *A. cyclops* seeds increases with time of exposure to 60°C. The lack of correlation between viability and alydid density at an inter-site level, despite within-site correlation, indicates that historical and environmental factors are more important determinants on a geographical scale.

The small seed bank found at the East London site is comparable to those in Australia (Gill & Neser 1984). However, this seed bank does not appear to be primarily the result of seed attack by *Z. acaciaphagus*. Rather, it appears that moist summer conditions, which contrast with the hot, dry summers experienced in its native habitat (Gill 1985), may increase rotting of *A. cyclops* seeds in the soil.

The finding that soil-seed density is not correlated with alydid density may reflect the low density of alydids present at most sites. Higher temperatures and rainfall (or related factors) appear to encourage seed bank decay. The large decreases measured in *A. cyclops* seed banks in the first year after the felling of mature stands (Holmes *et al.* 1987b) may largely be attributable to two processes: rotting and germination. Fresh seeds, damaged by alydids, rot soon after seed fall and therefore would not persist in the soil; hence the lower rotting of soil-stored seeds. Older seeds, especially those exposed to warm surface temperatures following removal of the stand, germinate more readily and would also deplete the seed bank.

Seed-feeding insects can be an important factor limiting the production of viable seeds (Waloff & Richards 1977; Schaefer 1980; Louda 1982; Harley 1985), yet few studies have demonstrated that they can influence plant recruitment (Louda 1982; De Steven 1982). Assuming that all rotting and seed deformity in this study was the result of alydid feeding, *Z. acaciaphagus* destroyed on average only 16% of the *A. cyclops* seed crop, compared to an equivalent alydid species in Australia which kills about 25% of the seed crop (van den Berg 1980). However, at Klipfontein, 84% of the seed crop was destroyed, indicating that alydids may have the potential to reduce the invasiveness of *A. cyclops*. Furthermore, since alydid populations increase through spring and summer, late maturing seeds are predisposed to greater attack (Gill 1985).

The wide variation in alydid predispersal seed attack, both within and between sites, highlights the difficulties in assessing the extent of seed loss to the plant species (Auld 1983; New 1983). The intensity of feeding reported here falls within the range for native seed predators and their hosts (Janzen 1971). Alone it may not be sufficient to reduce *A. cyclops* populations, but it may curtail the plant's invasiveness by reducing the number of viable seeds dispersed into 'safe sites' (c.f. Harper 1977). Costs of clearing operations would then decrease as a result of the lower rate of recruitment.

If the colonization of *A. cyclops* by *Z. acaciaphagus* is recent, as suggested by Holmes *et al.* (1987a), then the rate of accumulation of *A. cyclops* seeds in the soil should decrease over the next decade. A detailed study of *Z.*

acaciaphagus biology and population dynamics in *A. cyclops* stands is required to assess the importance of the alydids as potential controlling agents of this alien species.

Acknowledgements

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Appendix 1 Locality, stand density and mean temperature and rainfall data for 16 *Acacia cyclops* study sites in South Africa

	Site	Grid reference	Stand density (stems 100 m^{-2}) by stem diam. (cm)				Biomass (kg m^{-2})	Mean daily temperature (°C)			Mean rainfall (mm)	
			< 3	3–5	6–20	> 20		Max.	Min.	Mean	Annual	Summer
1	Klipfontein	32°01'S 18°31'E	0	7	10	5	22,0	25,7	11,0	18,4	145	11
2	Fairvlei	33°23'S 18°17'E	0	2	3	6	23,0	23,2	11,8	17,5	391	32
3	Koeberg	33°40'S 18°26'E	1	7	5	3	12,1	20,7	11,8	16,3	438	56
4	Rondevlei	34°05'S 18°29'E	1	6	16	2	7,5	21,4	11,6	16,5	525	33
5	Homestead	34°20'S 18°27'E	1	1	2	4	15,1	18,5	12,7	15,6	401	43
6	Walker Bay	34°25'S 19°20'E	26	59	40	0	4,8	20,0	13,9	16,9	452	61
7	Renosterkop	34°47'S 19°55'E	119	90	15	0	3,2	20,0	13,9	16,9	452	61
8	Arniston	34°35'S 20°15'E	129	36	20	0	4,0	20,0	13,9	16,9	452	61
9	Worcester	33°40'S 19°20'E	50	34	15	5	26,3	23,8	11,0	17,4	278	42
10	Albertinia	34°15'S 21°32'E	189	149	5	0	2,4	24,1	10,6	17,4	459	88
11	Goukamma	34°05'S 22°57'E	3	4	16	3	16,5	22,0	11,7	16,9	770	194
12	Keurboom	34°01'S 23°25'E	0	0	6	4	17,3	19,6	13,3	16,4	951	217
13	St. Francis	34°10'S 24°48'E	0	12	24	9	37,8	20,3	13,9	17,1	673	103
14	Port Elizabeth	34°03'S 25°28'E	48	178	52	0	10,2	22,2	12,7	17,5	662	114
15	Port Alfred	33°37'S 26°55'E	0	13	32	4	27,4	23,2	12,7	18,0	627	137
16	East London	32°52'S 27°48'E	0	0	2	4	14,5	22,7	14,0	18,4	849	241

(c) Post-dispersal seed removal

Paper 7. Holmes P.M. (submitted). Dispersal and predation of alien *Acacia* seeds: effects of season and invading stand density. S. Afr. J. Bot.

Dispersal and predation of alien Acacia seeds: effects of season and invading stand density

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Abstract

Acacia saligna and *A. cyclops* are invasive alien shrubs in lowland ecosystems of the fynbos biome, South Africa. Both species typically form dense thickets and accumulate large soil-stored seed banks. Seed removal rates, relative to seed availability in the litter layer of *Acacia*-infested vegetation, were studied to determine the importance of indigenous ants and vertebrates as dispersers and predators, respectively.

There was a relative loss to the annual seed-fall of 50% and 80-96% in dense *A. saligna* and *A. cyclops* stands, respectively. Ants and rodents removed significant quantities of seeds, but a large proportion may have rotted. In a dense *A. saligna* stand, ants usually removed all seeds presented to them after 7 days presentation, compared to only 36% of seeds in a dense *A. cyclops* stand. In dense stands of both species, rodents were relatively slow to take seeds, removing 31% within 7 days. Removal was least during and following seed-fall (January-March) and greatest prior to seed-fall (September-November) and decreased as *A. cyclops* canopy cover increased. In a low density *A. cyclops* stand, ants and rodents competed for seeds.

As large seed banks had accumulated under the dense *A. cyclops* stand only, predator satiation may have occurred and habitat alteration reduced the potential predator density. As rodents can potentially consume a large proportion of seeds at

low *Acacia* densities, I hypothesize that indigenous ants have played a critical role in maintaining and accumulating *Acacia* seed banks and thus may have facilitated the development of dense *Acacia* stands.

Key words: *Acacia cyclops* - *Acacia saligna* - ants - myrmecochory - rodents

Introduction

Many plant species have been translocated by man, but in order to establish, reproduce and become invasive in the area of introduction, they must be adapted to the new environment, survive interactions with resident competitors and predators, and re-establish any necessary mutualistic relationships (Kruger *et al.* 1986, Crawley 1987). Aliens may have the advantage over indigenes of having escaped from most of their coevolved pests and predators (Milton 1980, Mooney & Drake 1987), yet in order to invade new habitats, seed dispersal is essential (Salisbury 1961, quoted in Sorensen 1985).

The Australian shrubs, *Acacia saligna* (Labill.) Wendl. and *A. cyclops* A. Cunn. ex G. Don, have overcome habitat and biotic barriers to become serious invaders in lowland ecosystems of the fynbos biome, South Africa (Macdonald & Richardson 1986). They typically form dense thickets, suppressing the indigenous vegetation and thus reducing the species richness of the community (Richardson *et al.* 1989). Their success in South Africa has been variously attributed to their adaptability to different substrata (Taylor *et al.* 1985), rapid establishment after fire (Taylor 1983) aided by nitrogen-fixation (Milton 1980), efficient seed dispersal (Glyphis *et al.* 1981, Taylor *et al.* 1985, Knight 1988) and hard-coated seeds which accumulate in large soil-stored seed banks (Dean *et al.* 1986). As seed production in *A. cyclops* is similar in South Africa and Australia (Gill & Neser 1984), the much larger seed banks measured in South Africa may primarily relate to a low incidence of pre- and post-dispersal seed predation (Milton 1980, Milton & Hall 1981, Holmes & Rebelo 1988).

The *Acacia* dispersal unit is composed of the mature seed plus an expanded and elaborated portion of the funicle (O'Dowd & Gill 1986). In *A. saligna*, the funicle is a small, hard, white elaiosome. Seeds ripen in early summer, are shed soon after dehiscence in December, and, in Australia, are dispersed by ants (O'Dowd & Gill 1986). By contrast, in *A. cyclops* the funicle is a large, soft, red aril encircling the seed (O'Dowd & Gill 1986). Ripening is more protracted and

precedes a five month display period during which bird-dispersal occurs (Knight 1986). In Australia, seeds are dispersed by both birds and ants (O'Dowd & Gill 1986).

Seeds of both *Acacia* species, but especially those of *A. cyclops*, are dispersed by birds in South Africa (Middlemiss 1963, Glyphis *et al.* 1981, Knight 1988). *Acacia cyclops* seeds are also dispersed by Chacma Baboons (*Papio ursinus* Kerr) (Middlemiss 1963). Efficient dispersal by rodents is unlikely as there are no seed-caching species in fynbos (Slingsby & Bond 1985), and dispersal by ants is thought to be unimportant (Milton & Hall 1981), despite the high incidence of myrmecochory (diaspore dispersal by ants) in the Cape flora (Bond & Slingsby 1983).

In Australia, pre-dispersal seed predation by several species of Hemiptera, Coleoptera and Lepidoptera results in large, though variable, losses to the annual seed production (van den Berg 1980a,b,c). Some Hemiptera may also feed on seeds beneath trees (van den Berg 1980c). Despite their role as dispersers of *A. cyclops* seeds, birds may be major predators of immature seeds (Gill 1985). However, there is no record of any Australian vertebrate being an important post-dispersal seed predator of either species.

In South Africa, potential *Acacia* seed predators on the ground are granivorous birds such as the doves *Streptopelia senegalensis* (L.) and *S. capicola* (Sundevall) (Winterbottom 1970, Glyphis *et al.* 1981), and rodents, particularly the striped fieldmouse (*Rhabdomys pumilio* (Sparrman)) and, in sandy soils, the gerbil (*Tatera afra* (Gray)) (David 1980). Hemipterans (*Zulubius acaciaphagus* Schaffner) and larvae of one species of Lepidoptera are the only invertebrates recorded as

destroying *A. cyclops* seeds in South Africa (Milton 1980, Holmes *et al.* 1987, Holmes & Rebelo 1988), none being known for *A. saligna*.

In this study, *Acacia* seed removal rates in the litter layer of *Acacia*-infested vegetation were investigated, with particular reference to the following questions:

1) Is seed dispersal by indigenous ants significant and does it depend upon presence of the aril in *A. cyclops*?

2) Do vertebrates eat significant numbers of *Acacia* seeds?

3) Are seed removal rates dependent upon seed availability in the litter layer (i.e. *Acacia* stand density and seasonal seed supply)?

Study sites and methods

Experimental sites were established in the Silvermine (34o05'S 18o41'E), Cape of Good Hope (CGHNR:34o20'S 18o28'E) and Goukamma (34o03'S 22o57'E) nature reserves. Mesic mountain fynbos vegetation on shallow, nutrient-poor soils, derived from Table Mountain Sandstone (Moll *et al.* 1984), occurs at both Silvermine and CGHNR. Both have a Mediterranean-type climate, with warm dry summers and cool wet winters (Fuggle 1981). A mosaic of dune fynbos and kaffrarian thicket on deep recent sands (Moll *et al.* 1984) occurs at Goukamma, which experiences all-year rainfall (Fuggle 1981). The mean annual rainfall is 750 mm at both CGHNR and Goukamma and 900 mm at Silvermine (South Africa 1:250 000 rainfall maps, 1965). Sites had been subject to invasion by acacias for at least 25 years, as determined from aerial photographs.

At Silvermine a single 1 ha. plot was demarcated in a dense stand (projected canopy cover (PCC) of 100%) of *Acacia saligna*. At CGHNR, three 1 ha. plots in 10%, 72% and 100% PCC stands of *Acacia cyclops* were demarcated, all within an area of 0.5 square km in similar terrain. PCC was used as a measure of stand density, and in *A. cyclops* plots, was determined using the line intercept method (M W Fraser pers. comm.). The dense stands differed, in that *A. saligna* had an open understorey with some indigenous species persisting, whereas *A. cyclops* formed a

thicker canopy precluding undergrowth. A dense *A. cyclops* stand at Goukamma was used only for collecting seed-fall data.

Gross annual seed-fall and seed-loss were assessed using five pairs of randomly located traps in the dense stand of each species and a further 10 pairs of traps in the dense Goukamma stand. Traps consisted of shadescreen fabric attached to 0.5 m-diameter metal rings. A shallow tray open to seed removal in the litter layer was made by pulling fabric tightly across the ring, and in the other half of the pair, fabric was attached to the ring to form a deep bag, which was then suspended from a tree to minimize seed removal. Traps were positioned in November 1985, before seed-fall, and were lifted after 9 months (*A. saligna*) and 12 months (*A. cyclops*). Net loss after seed-fall was taken to be the difference in seed content between the two types of trap.

Seed removal rates by ants and vertebrates were assessed by presenting replicates of twenty seeds of the respective species on plywood trays (10 X 10 cm) in the litter layer of each plot, and giving one of four treatments, as follows:

1) no exclosure (open to ants and vertebrates);

2) chicken wire (0.5 cm) cage pegged over tray (to exclude vertebrates);

3) tray rim smeared with formex gel (to exclude crawling invertebrates, predominantly ants);

4) treatments 2) and 3) combined (control, to exclude both ants and vertebrates).

Seeds for use in trials were gathered following dehiscence, in December 1985, from trees within study areas, and stored in the laboratory in open bags. Seeds of *A. saligna* were presented intact, whereas half the *A. cyclops* seeds (i.e. 10 per tray) were hand-stripped of their arils. Five presentations (replicates) of the four treatments were placed at random locations within each plot and these locations tagged for future trials. Trays were placed during the morning and

checked 24 hours and 7 days later, after which they were removed. This trial was repeated on a bimonthly basis in order to assess seasonality of removal rates.

Acacia seed banks were estimated by removing soil samples (*A. cyclops*: 20 cores of 5 cm-diameter X 10 cm deep; *A. saligna*: 25 samples of 25 X 25 cm to bedrock) beneath the *Acacia* canopies in each plot. Samples were sieved and seeds extracted. In addition, an *A. cyclops* plot of 42% PCC was sampled within the 0.5 square km area of the other CGHNR plots. Assuming negligible dispersal beyond the perimeter of *A. cyclops* canopies, these estimates were recalculated as average seeds.m^{-2} over the entire plot and plotted together with the seed input estimates.

Differences in seed contents between trays and bags were tested by the randomization test for matched pairs (Siegel 1956). In the removal rate experiment, counts of seeds removed were square-root transformed to equilibrate the variance. The effects of ants, vertebrates and season on removal rates were analysed for each plot separately, and for the two dense stands together, using two-way ANOVA with repeated measures (Programme BMDP2V, Dixon 1985). The effect of aril on *A. cyclops* removal rates was tested using the same ANOVA programme which included a split-plot design.

It must be emphasized that the seed removal experiment is pseudoreplicated (*sensu* Hurlbert 1984) and possible inter-site variation was not allowed for in the design. However, the plots of different *A. cyclops* density were located close together in the same habitat, thus minimizing the effects of factors other than density; and species comparisons are not generally possible at the one site. Ideally, more sites should have been sampled across a wider range of habitats.

The results should be treated as preliminary, and may be less applicable to areas outside the Cape Peninsula.

Results

Relative seed loss in the litter layer

Annual seed-fall in dense *A. cyclops* stands was estimated to be 800 and 1300 seeds.m^{-2}, at CGHNR and Goukamma respectively; and in the dense *A. saligna* stand 2100 seeds.m^{-2} (Table 1). Differences in seed contents between bags and trays (i.e. closed *versus* open to seed removal agents) were significant at all three sites ($P < 0.05$, randomization test for matched pairs) and indicated a relative loss to annual production of 80-96% (*A. cyclops*) and 50% (*A. saligna*) in the litter layer (Table 1). Analysis of seed remains indicated that predation was reduced, but not excluded, by the bags: at Goukamma, 22% of seeds were destroyed in the bags, compared to 74% in the trays, by rodent predation. A portion of the seeds were also deformed or decayed, although none were germinating: these amounted to 26% in the bags and 11% in the trays (Table 1).

Seed removal in dense *Acacia* stands

In dense stands, seed removal by ants exceeded that by vertebrates (Tables 2 & 3, Fig. 1): in *A. saligna* averaging 78% and 94% of presented seeds after 24 hours and 7 days respectively, *versus* 10% and 31%; and in *A. cyclops* 12% and 35% *versus* 5% and 31%. The pattern of seed removal differed between the two species (ANOVA, $F = 228.3$, $P < 0.0001$): under *A. saligna* it was generally rapid and complete, primarily as a result of ant activity, whereas it was generally slow and incomplete under *A. cyclops* (Fig. 1). Ground-feeding vertebrates removed a significant portion of *A. cyclops* seeds within 24 hours, but only after 7 days in *A. saligna* (Tables 2 & 3). There was an interaction effect only in the *A. saligna* stand after 7 days (ANOVA, ants X vertebrates, $F = 17.1$, $P < 0.005$, Table 3). Small losses from

Table 1 Mean seed density (seeds.m^{-2} ± SD) in bags (removal minimized) and trays (open to removal agents) 9 months (*A. saligna*) and 12 months (*A. cyclops*) after seed-fall.

Site	Species	Bags	Trays	% Loss in litter
Silvermine	*A. saligna* intact seed	2102±2020 (n=5)	1087±1465* (n=4)	48.3
Cape of Good Hope	*A. cyclops* intact seed	780±220 (n=5)	162±77* (n=5)	79.2
Goukamma	*A. cyclops* intact seed	695±618 (n=8)	30±54* (n=9)	95.7
	deformed or decayed seed	316±176	21±20	-
	seed remnants produced by rodents	296±334	146±174	-

*Difference between bags and trays significant $P < 0.05$ (randomization test for matched pairs).

Table 2. Two-way analysis of variance with repeated measures on square-root transformed counts of Acacia seeds removed after 24 hours. Separate analyses for three A. cyclops stands of different canopy cover and a dense A. saligna stand (NS $P > 0.05$, * $0.05 > P > 0.005$, ** $0.005 > P > 0.0005$, *** $P < 0.0005$).

		Acacia cyclops						*Acacia saligna*	
		10% PCC		72% PCC		100% PCC		100% PCC	
Effect	df	SS	F	SS	F	SS	F	SS	F
ants	1	93.1	80.5***	77.8	41.1***	22.5	34.7***	289.2	565.1***
vertebrates	1	91.5	78.4***	88.1	46.6***	7.0	10.8**	1.1	2.2NS
ant X vert	1	29.1	25.0***	3.0	1.6NS	0.1	0.1NS	0.8	1.6NS
error	16	18.7		30.3		10.4		8.2	
season	5	13.8	3.4*	66.2	10.6***	71.8	22.1***	57.8	17.5***
sea X ant	5	15.3	3.8**	8.5	1.4NS	24.0	7.4***	31.1	9.4***
sea X vert	5	19.6	4.8**	22.2	3.5*	9.9	3.1*	1.5	0.5NS
s X a X v	5	5.7	1.4NS	5.7	0.9NS	5.6	1.7NS	2.2	0.7NS
error	80	64.8		100.4		52.0		52.8	

Table 3. Two-way analysis of variance with repeated measures on square-root transformed counts of *Acacia* seeds removed after 7 days. Separate analyses for three *A. cyclops* stands of different canopy cover and a dense *A. saligna* stand (NS $P>0.05$, * $0.05>P>0.005$, ** $0.005>P>0.0005$, *** $P<0.0005$).

	Acacia cyclops							*Acacia saligna*		
	10% PCC			72% PCC		100% PCC		100% PCC		
Effect	df	SS	F	SS	F	SS	F	df	SS	F
ants	1	49.7	126.9***	61.1	125.0***	74.0	62.5***	1	201.2	706.0***
vertebrates	1	36.7	93.6***	40.7	83.3***	50.9	43.0***	1	7.0	24.7***
ant X vert	1	29.8	76.2***	8.2	16.8**	0.5	0.4NS	1	4.9	17.1**
error	16	6.3		7.8		18.9		16	4.6	
season	4	7.2	11.0***	74.6	26.6***	62.7	15.3***	5	21.0	7.9***
sea X ant	4	4.9	7.4***	4.9	1.8NS	7.2	1.8NS	5	17.5	6.5***
sea X vert	4	4.5	6.8***	2.2	0.77NS	4.5	1.1NS	5	1.5	0.4NS
s X a X v	4	4.4	6.6***	3.1	1.1NS	5.1	1.2NS	5	2.0	0.8NS
error	64	10.6		44.7		65.5		80	42.9	

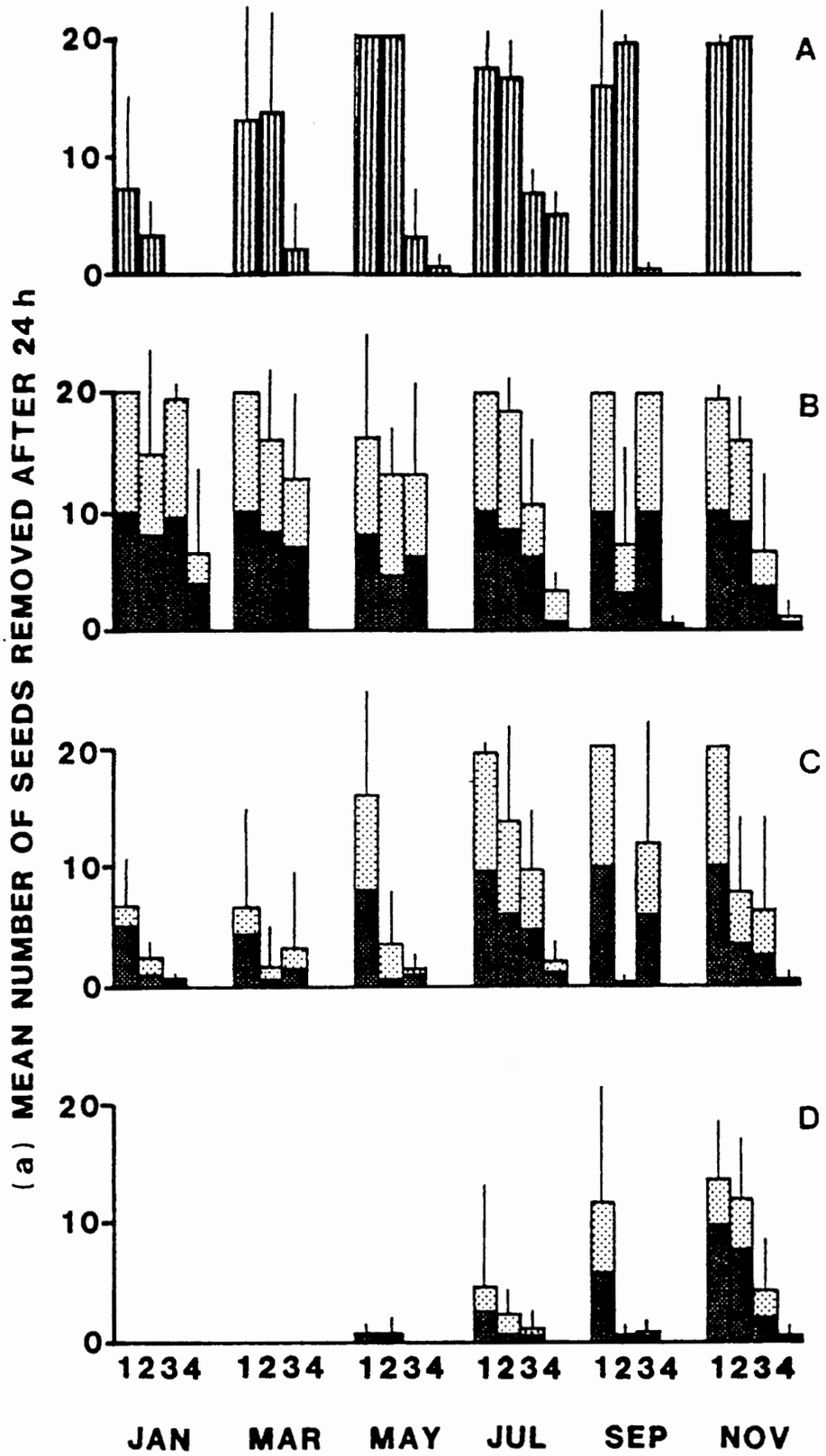
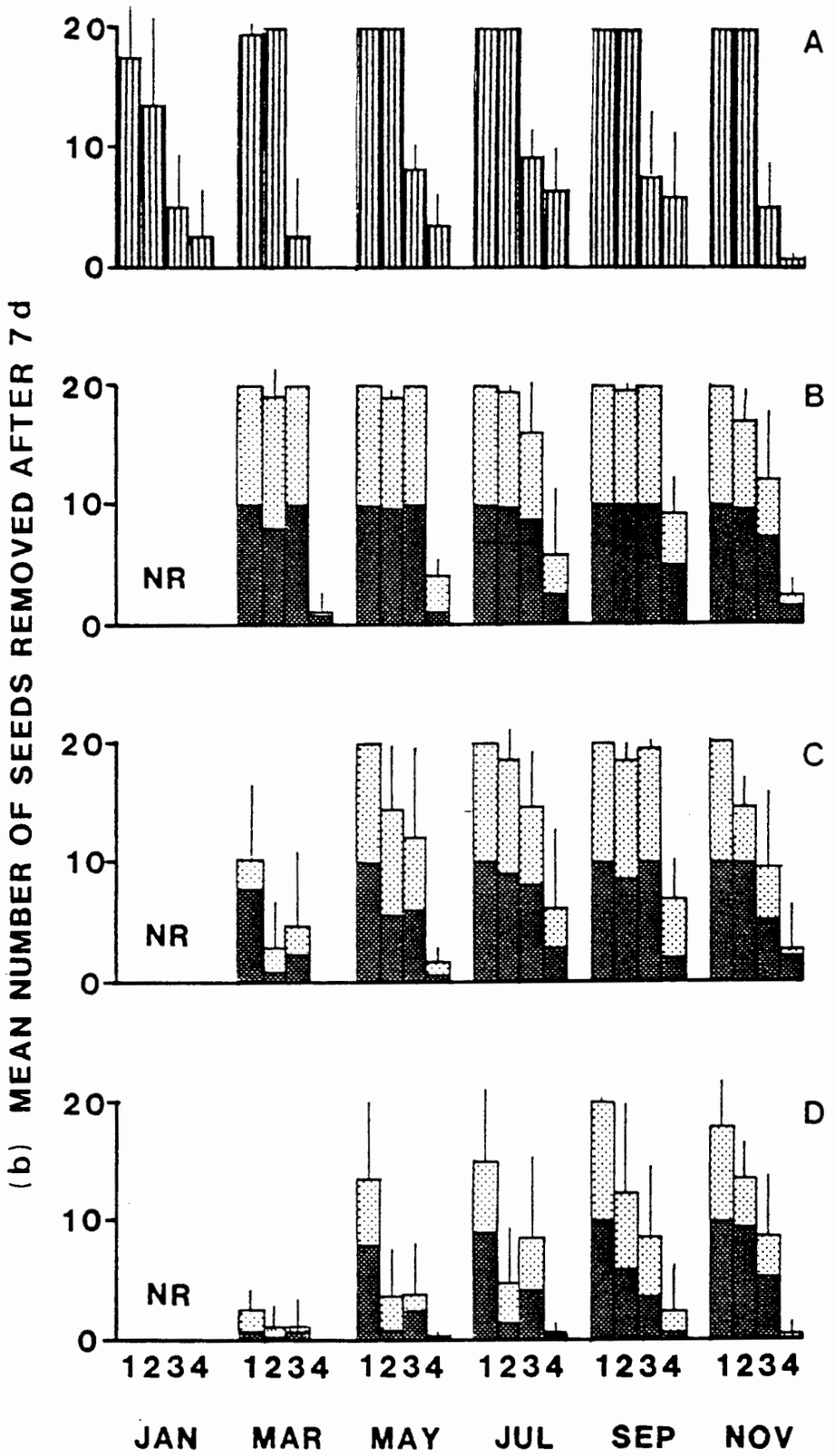


Fig. 1. Seed removal after (a) 24 hours and (b) 7 days (mean number out of 20 seeds ± SD, n=5) at six times of year from trays with different exclosures (1=open, 2=excluding vertebrates, 3=excluding ants, 4=excluding all) in a dense *A. saligna* plot (A) and three *A. cyclops* plots of different PCC (B=10%, C=72%, D=100%). *Acacia saligna* seeds+elaiosomes (striped); *A. cyclops*: seeds+arils (shaded), seeds-arils (stippled); NR=not recorded.



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control trays were indicative of occasional disruption, especially after 7 days: e.g. litter debris blown onto formex giving access to ants and heavy rain dislodging seeds from trays.

Effect of seed availability on removal

Seed removal varied significantly with season in all stands (Tables 2 & 3). Removal was lowest during and following seed-fall (January-March) and greatest prior to seed-fall (September-November) (Fig. 1). In dense stands, seed removal by ants after 24 hours showed seasonal variation, whereas removal by vertebrates varied seasonally only in *A. cyclops* (Tables 2 & 3). Among *A. cyclops* stands, the low density stand gave least seasonal variation in seed removal (ANOVA, after 24 hours, $F=3.41$, $P<0.05$, compared to $F=10.6$ & $F=22.1$, $P<0.0005$, for 72% & 100% PCC stands, respectively; Table 2).

Seed removal decreased as *A. cyclops* canopy cover increased (Fig. 1). After 24 hours, ants and vertebrates had removed similar portions of seeds in 10% and 72% PCC stands, whereas in the dense stand, ants were more efficient than vertebrates (Table 2). There was an interaction between ants and vertebrates in the low density stand only (ANOVA, $F=25.0$, $P<0.0005$, Table 2). After 7 days, ants and vertebrates were highly significant seed removers in all three stands, with a significant interaction in all except the dense stand (Table 3).

Effect of aril on *A. cyclops* seed removal

There was no consistent preference by ants or vertebrates for *A. cyclops* seeds with or without arils (Fig. 1; ANOVA, $P>0.2$ after 24 hours and 7 days in all stands).

Seed banks in relation to *Acacia* canopy cover

Acacia cyclops seed banks were estimated to be 76 ± 41, 1579 ± 530, 1095 ± 357 and 5170 ± 688 ($\bar{x} \pm$ S.D.) seeds.m^{-2} under the *Acacia canopy* in 10%, 42%, 72% and 100% PCC stands, respectively, compared to 7920 ± 560 seeds.m^{-2} under dense *A.*

saligna. In the low density stand, annual seed-fall exceeded soil-seed density, whereas in the two intermediate stands, the soil-stored component parallelled seed input (Fig. 2). However, in the dense stand, soil-seed density exceeded annual seed-fall by a factor of six (Fig. 2).

Discussion

A large proportion of seeds are lost in the litter layer of dense *Acacia* stands. More seeds are lost via dispersal than predation: however, decay rates in buried seed populations average 45% and 97% in *A. saligna* and *A. cyclops*, respectively during the first year (Holmes 1989), indicating that rotting might be the major process occurring in dense thickets.

Dispersal by ants

Ants were observed removing seeds of both species from trays, sometimes within 10 minutes of placement. The species involved probably belong to the widespread fynbos genera *Anaplolepis* and *Pheidole*, which rapidly remove and bury myrmecochorous seeds in subterranean nests (Bond & Slingsby 1983). Seeds of another invasive alien species, *Acacia longifolia* (Andr.) Willd., are also removed by ants (Pieterse & Cairns in press). That alien acacias have established mutualistic relations with indigenous ants ensures both 'escape' and 'directed' dispersal (Howe & Smallwood 1982), and highlights the convergent evolution of diaspore dispersal in Australia and South Africa (Milewski & Bond 1982). It also indicates that diffuse coevolution (Herrera 1985) between plants and invertebrate disperser species may occur. However, as these ants seldom carry seeds a distance exceeding 2-3 m (Bond & Slingsby 1983), they are more important in maintaining *Acacia* soil-stored seed banks than in extending their invasive front. Whilst ants disperse *Acacia* seeds over short distances and birds may disperse them over a few hundred

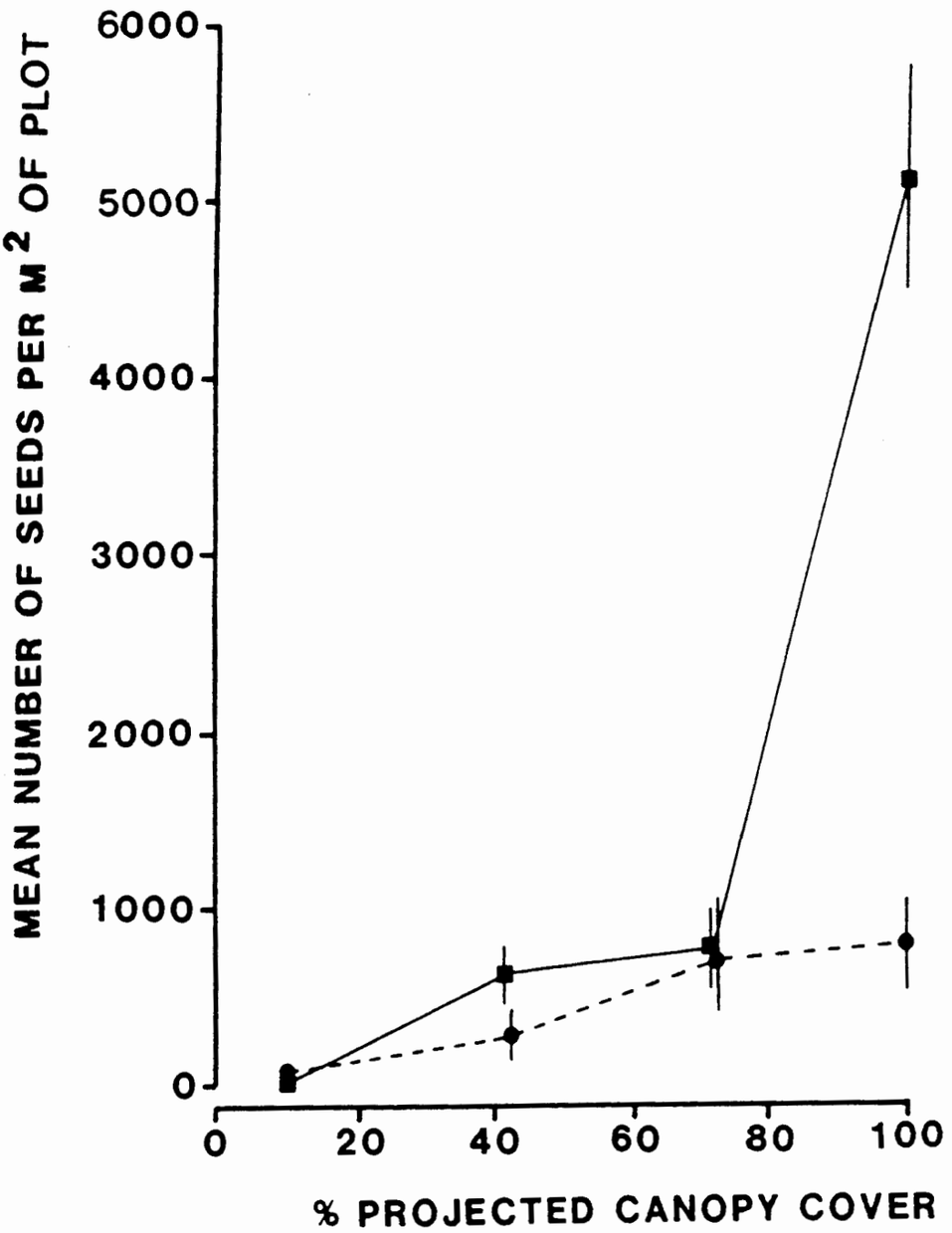

Fig. 2. The relationship between soil-seed density (■ seeds.m^{-2} + SD, n = 20 cores) and annual seed-fall (● seeds. m^{-2} + SD, n = 10 traps (R S Knight & M W Fraser, unpublished), except in 100% PCC plot where n = 5 traps) in 1 ha. plots of different *A. cyclops* canopy cover at the CGHNR.

metres (Glyphis *et al.* 1981, Gill 1985), mankind is responsible for the widespread dispersal of these aliens in South Africa (Shaughnessy 1986).

Seeds of A. *saligna* are six times more likely to be taken by ants in the first 24 hours than those of *A. cyclops*. Possibly the thicker canopy in the dense *A. cyclops* stand may have significantly reduced ant activity relative to that of the dense *A. saligna* stand. Shading by an encroaching spruce/pine plantation has been shown to drastically reduce the number of ant colonies in northern temperate regions (Seeley & Heinrich 1981).

The lack of an overall preference by ants for seeds with arils suggests that the aril does not contain a coevolved attractant for the indigenous ants (Bond & Slingsby 1983) and is removed as a food item only if encountered. However, after hand-stripping, a trace of aril may remain attached to the seed, and this may have been a sufficient attractant to the ants (cf. Bond & Breytenbach 1985).

Predation by vertebrates

Vertebrates removed a significant quantity of *Acacia* seeds, although rate of removal was low in dense stands: when ants were excluded, an average of 10% and 5% were removed in *A. saligna* and *A. cyclops* stands, respectively, after 24 hours. The striped fieldmouse (*Rhabdomys pumilio*) was encountered in the study areas and seemed to be the principal vertebrate seed predator. All seed remnants in or adjacent to plywood trays were typical of those produced by small mammals. There was no evidence of gerbils (*Tatera afra*) being present: soils in the study plots are probably too shallow and rocky for its burrowing activities (Smithers 1983). Avian granivores are rare in mountain fynbos vegetation (Siegfried 1983) and although more common in *Acacia* thickets (Winterbottom 1970), none were encountered during trials.

Studies on *Rhabdomys pumilio* in a mixed *A. saligna* and *A. cyclops* stand (45% total *Acacia* PCC) on the Cape Flats indicate that, on average, *Acacia* seeds form 50% of its diet, with a daily consumption of about 5 g ($\pm$125 *A. cyclops* or

±250 *A. saligna*) of seeds (David 1980). The minimum population size calculated from a continuous five-year census was 33-256 individuals.ha.$^{-1}$ (David & Jarvis 1985). Based on these figures, *R. pumilio* consumes a minimum of 151-1168 seeds.m^{-2}.y^{-1} (*A. cyclops*) or 301-2336 seeds.m^{-2}. y^{-1} (*A. saligna*). If *R. pumilio* populations are unaffected by altered vegetation structure in dense *Acacia* stands, they have the potential to consume the entire *Acacia* seed crop. Clearly this does not occur, as large seed banks have accumulated in the dense stands. However, the relatively small seed banks measured in *A. cyclops* stands up to 72% PCC suggests that *R. pumilio* may consume a large proportion of the seeds. That there is such a large disparity in soil-stored seed density between 72% and 100% PCC stands indicates not only that predator satiation is occurring, but also that habitat alteration, possibly a reduction in suitable nesting habitat (grass tussocks, Smithers 1983), is reducing the potential *R. pumilio* density.

Effect of seed availability on removal

Both seasonal abundance of seeds and increasing seed-rain at higher stand densities results in decreased removal. Although seeds are available in the litter layer of dense stands throughout the year, it appears that the laboratory-stored seeds are preferred in the latter half of the year, possibly because arils and elaiosomes deteriorate more quickly in the field. Alternatively, seeds presented at the surface may be more eagerly sought when the only alternative source is buried beneath the litter.

In the low density stand there was some evidence that ants and rodents compete for seeds: in presentations open exclusively to them, an average of 72% and 76% of seeds, respectively, were removed after 24 hours. Ants are generally faster at locating and removing seeds than rodents (Bond & Breytenbach 1985) and may take a larger proportion of seeds falling into the litter layer if seeds are in short supply. Predation levels in dense *A. saligna* and *A. cyclops* stands are similar,

and it is likely that reduced canopy cover in *A. saligna* would lead to a relative increase in predation rates as found in *A. cyclops* stands.

Implications of dispersal and predation for *Acacia* seed bank dynamics

In fynbos habitats being invaded by acacias, resident rodent populations could potentially consume the entire *Acacia* seed crop, thus reducing the invasiveness of the species, were it not for the presence of ants which rapidly move seeds below ground to their nests. Just as ants are important in maintaining seed banks of indigenous proteaceae (Bond & Slingsby 1984, Bond & Breytenbach 1985), they might have played a critical role in maintaining and accumulating alien *Acacia* seed banks. Whilst the acacias have been spread into uninfested habitats by generalist frugivores (Glyphis *et al.* 1981, Knight 1988), they appear to be pre-adapted to the local short-distance dispersal-mutualism. The significance of this is firstly, that seeds escape rodent predation, and secondly, in a fire-prone vegetation-type such as fynbos, populations are protected from fire: especially important for non-resprouting *A. cyclops*. If *Acacia* seeds are buried alongside indigenous seeds, their rapid germination after fire (Milton 1980, Taylor 1983, Jeffery *et al.* 1988) may give them a competitive edge over the indigenous species. Together with a high production of relatively non-parasitized, undamaged seeds (Milton 1980, Holmes & Rebelo 1988), this may enable the acacias to accumulate larger soil-stored seed banks than the indigenes, resulting in the aliens rapidly forming dense stands with successive fires. The possible deleterious effects of the presence of alien acacias on the indigenous ant-plant mutualism remains to be investigated.

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(d) Seed burial and its effects

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Paper 10. Holmes P.M. (submitted). Vertical movement of soil-stored seeds at a sandplain fynbos site. S. Afr. J. Ecol.

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Decay rates in buried alien *Acacia* seed populations of different density

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Decay rates in seed populations of *Acacia cyclops* and *A. saligna* of known viability and dormancy were determined after one and two years of burial at different densities. Decay rates differed significantly between the two species, but there was no clear effect of density. Decay rates were high, despite an initially high level of dormancy: an average of 97% and 45% of *A. cyclops* and *A. saligna* seeds, respectively, were lost in the first year. Decay rates were significantly lower in the second than in the first year and it is predicted that decay rates would continue to decline in seeds surviving more than two years. *Acacia* seed populations in the soil do not have a continuous and constant death risk and consequently do not fit the log-linear (i.e. Deevey Type II) survivorship curve reported in the literature for soil-stored seeds. As a small proportion of the *Acacia* seed population may have great longevity, clearing operations should incorporate a programme of periodic follow-up control.

Afbraaksnelhede van saad van *A. cyclops* en *A. saligna*, waarvan die lewensvatbaarheid en rustoestand bekend is, is na een en twee jaar nadat dit in verskillende digthede begrawe is, bepaal. 'n Aansienlike verskil in afbraaksnelhede tussen die twee spesies is opgemerk, maar daar was nie 'n merkbare uitwerking op die digtheid te bespeur nie. Afbraaksnelhede was hoog, ten spyte van aanvanklike hoë rustoestandsvlakke: 'n gemiddelde van 97% en 45% van *A. cyclops*- en *A. saligna*-saad onderskeidelik, het gedurende die eerste jaar verlore gegaan. Afbraaksnelhede was opvallend minder in die tweede jaar as in die eerste jaar. 'n Voortgesette daling van afbraaksnelhede by sade wat vir meer as twee jaar oorleef het, word voorspel. *Acacia*-saad in die grond het nie 'n aaneenlopende en konstante sterflikheidsrisiko nie en gevolglik pas hulle nie in die patroon van log-lineêre oorlewingskromme (bv. Deevey Type II), soos in die literatuur vermeld is vir ondergrondsgebergde saad nie. Vanweë die feit dat 'n klein persentasie van *Acacia*-saad 'n hoë lewensverwagting kan hê, word daar aanbeveel dat uitdunningsoperasies deur periodieke opvolgaksies ondersteun word.

Keywords: *Acacia cyclops*, *Acacia saligna*, dormancy, longevity, survivorship models

Introduction

Invasion by Australian *Acacia* species is a major threat to remaining vegetation in the fynbos biome, South Africa, with *Acacia saligna* (Labill.) Wendl. and *A. cyclops* A. Cunn ex G. Don, being the most widespread invaders in lowland ecosystems (Macdonald & Richardson 1986). These invasive acacias owe much of their success to a prolific production of hard-coated seeds, which accumulate in large soil-stored seed banks (Dean *et al.* 1986). Seed longevity in the soil is a pertinent factor in assessing the seriousness of a weed problem (Egley & Chandler 1978). Seed longevity is often associated with water-impermeability (Rolston 1978), and may exceed 50 years in some Australian *Acacia* species (Cavanagh 1980). *Acacia* seeds therefore remain dormant, ensuring temporal and spatial survival (Rolston 1978). Soil-seed populations are generally assumed to have a continuous and constant death risk (Roberts 1972; Harper 1977) which varies with species and management (Sagar & Mortimer 1976), allowing longevity of a seed population to be inferred from decay rates of fresh seeds buried in the soil. Knowledge of alien *Acacia* seed decay rates and potential longevity in South Africa may help to identify optimal control strategies. In this study, decay rates of fresh *A. saligna* and *A. cyclops* seeds in the soil were quantified after 1 and 2 years of burial. The study incorporated a seed-density component to determine pathogenic, inhibitory or other density-dependent factors which may influence decay rate.

Methods

The study was undertaken at the Pella Fynbos Biome Research Site (31°31'S, 18°32'E), 62 km north-east of Cape Town. Pella has a true Mediterranean, warm-temperate climate (Koppen's climatic type Cs) with over 70% of the rainfall occurring between April and September (Jarman 1988). Annual rainfall averaged 600 mm during the study period (January 1985 – March 1987). The area supported 5-year-old sandplain lowland fynbos vegetation, dominated by evergreen shrubs and Restionaceae, on acidic, sandy soil of the Clovelly form (Stock & Lewis 1986).

Ripe seeds were collected from dehisced pods on *Acacia saligna* and *A. cyclops* trees at Pella during December 1984 and January 1985. Sub-samples ($n = 5 \times 25$ seeds) were tested for germinability and viability using methods described in Holmes & Rebelo (1988). Seeds were mixed with coarsely sieved soil in fibreglass gauze (2-mm mesh) bags, placed in tagged cylinders of brass screening (3.3-mm mesh and *ca.* 800 cm^3 volume) to exclude predators, and then buried 10–50 mm deep in gaps between fynbos plants at the end of January 1985. Seeds were grouped into five different densities (*A. saligna*, 10–200 seeds per cylinder; *A. cyclops*, 10–150 seeds per cylinder; Table 1) encompassing the range measured under stands of the invaders (*A. saligna*, up to

Table 1 Decay rates of *Acacia* seeds in the soil (mean no. of seeds per container ± *S.D.*) 1 and 2 years after burial at different densities

		0–1 years			1–2 years			0–2 years		
	Initial seed	Decayed		%	Decayed		%	Decayed		%
N	density	Mean±*S.D.*	Range	decayed	Mean±*S.D.*	Range	decayed	Mean±*S.D.*	Range	decayed
Acacia cyclops										
10	10	9.9±0.3	9–10	99.0	0	0	0	9.9±0.3	9–10	99.0
10	20	19.4±0.7	18–20	97.0	1.2±0.4	1–2	100	20.0±0.0	–	100
5	50	49.0±1.0	48–50	98.0	0.7±0.6	0–1	40.0	49.4±0.9	48–50	98.8
5	100	98.8±1.1	97–100	98.8	1.0±0.8	0–2	66.6	99.6±0.5	99–100	99.6
5	150	141.4±2.3	134–147	94.2	6.4±3.0	2–10	74.4	147.8±2.4	144–150	98.5
Acacia saligna										
10	10	4.7±1.3	3–7	47.0	1.1±0.9	0–3	20.8	5.8±1.5	4–8	58.0
10	50	20.4±5.4	14–29	40.8	4.8±2.3	2–9	16.2	25.2±5.8	16–34	50.4
5	100	39.6±5.1	34–46	39.6	10.4±9.8	3–27	17.2	50.0±12.5	48–71	50.0
5	150	77.4±14.3	63–101	51.6	9.0±3.8	7–15	12.9	86.8±17.0	74–116	57.9
5	200	91.4±15.8	77–111	45.7	15.4±10.7	4–29	14.2	106.8±20.6	88–140	53.4

13 800 seeds m^{-2}; *A. cyclops*, up to 5 900 seeds m^{-2}; Milton & Hall 1981). Cylinders were recovered in early March 1986 for enumeration of seed remains, then reburied with the intact seeds and recovered again in early March 1987 for a second enumeration. Additional cohorts of seeds were buried in 1986 for bimonthly assessment of decay.

Proportions of surviving seeds were arcsine-transformed and differences in decay rate among density classes and between species were tested by analysis of variance (program BMDP7D, Dixon 1985). The Mann–Whitney U test (Siegel 1956) was used to test for differences in percentage decay between years.

The probabilities of survival measured in this study, together with data on seed fall under *Acacia* stands (Milton & Hall 1981) were used in matrix models (Begon & Mortimer 1986) to predict equilibrium seed bank populations and seed bank decay rates in the absence of seed fall.

Results

Percentage viabilities of seed populations used in the study were 84.0% ± 4.9 for *A. cyclops* and 100% ± 0 for *A. saligna*, with respective percentage germinabilities (i.e. viable nondormant portions) of 8.8% ± 6.6 and 10.4% ± 3.6 (means ± *S.D.*, $n = 5 \times 25$ seeds).

In *A. cyclops*, percentage decay averaged 96.6% and 72.1%, for 0–1 and 1–2 years respectively, compared to 45.4% and 14.9% in *A. saligna* (Table 1). Species explained most of the variance in the data (ANOVA, $P<0.0001$, after 1 and 2 years), whereas there was no significant density effect (ANOVA, $P>0.40$, after 1 and 2 years) (Table 2). However, the pattern was less clear when seeds surviving after 2 years were expressed as a proportion of those surviving after 1 year: a significant interaction between species and seed density (ANOVA $P<0.05$, Table 2) is attributable to the few *A. cyclops* seeds surviving in low density classes after 1 year. Probability of survival was greater in the second than in the first year (U test, $P=0.075$, *A. cyclops*; $P=0.004$, *A. saligna*).

In 1986, most seed bank decay occurred during Autumn (April – May) and Summer (December – March) (Figure 1).

Seed survivorship models

Values for seed fall and probability of survival used in the matrix models are presented in Table 3. Those seeds

Table 2 Analysis of variance on arcsine-transformed proportions of *Acacia* seeds remaining in the soil

	0–1 years				1–2 years				0–2 years			
Source	*df*	*SS*	*F*	*P*	*df*	*SS*	*F*	*P*	*df*	*SS*	*F*	*P*
Species	1	3.94	398.03	<0.0001	1	0.49	3.52	0.069	1	2.74	232.42	<0.0001
Density	3	0.03	0.87	0.464	3	1.15	2.76	0.057	3	0.02	0.66	0.582
Sp. X den.	3	0.06	1.90	0.142	3	1.38	3.31	0.031	3	0.03	0.76	0.521
Error	47	0.47			35	4.86			47	0.55		

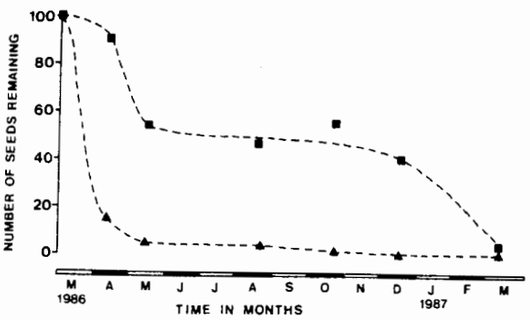

Figure 1 Patterns of survival in 1986 seed cohorts of *A. saligna* (triangles) and *A. cyclops* (squares) during 1986. Destructive sampling of six batches of 100 seeds per species (no replication).

surviving the first 2 years were assumed to have the same probability of survival as in the second year (model A) or a probability of survival of 0.9 (model B), the latter based on the hypothesis that probability of seed survival increases with duration of burial. The models generate equilibrium seed populations of (A) 24 153 and (B) 33 583 seeds m^{-2} for *A. saligna* compared to (A) 1 251 and (B) 1 351 seeds m^{-2} for *A. cyclops*. These seed densities are all within the ranges measured under dense stands of the species, except for the first *A. cyclops* figure, which is rather low (Holmes *et al.* 1987). As much larger seed banks have been measured for both species, it is plausible that probability of survival increases with time in the soil, and in *A. cyclops* may approach 1.0 after 2 years.

The seed survivorship curves generated by the models in the absence of seed inputs, are compared to curves based on measured seed bank decline following the felling of *Acacia* stands (Holmes *et al.* 1987) (Figure 2). Models for *A. saligna* generate shallower curves than the measured seed bank decline. In *A. cyclops* steeper curves are generated by the models, with only model B approximating the magnitude and pattern of seed survivorship following felling.

Discussion

Depletion of the soil seed bank is dependent upon rates of germination, mortality and predation (Weaver & Cavers 1979). As predation was excluded in this study,

Table 3 Annual seed fall and seed survival probabilities used in the matrix models

Species	Annual input (seeds m^{-2})	Probability of survival			
		0–1 years	1–2 years	3+ years A	3+ years B
A. cyclops	1197*	0.03	0.33	0.33	0.9
A. saligna	5443*	0.55	0.84	0.84	0.9

*seed inputs are from Milton & Hall (1981)

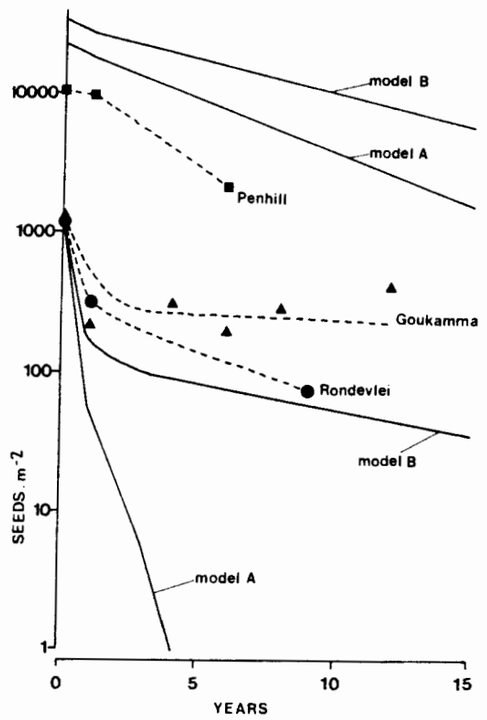

Figure 2 Seed survivorship curves generated by matrix models (solid lines; see text for further details) and following felling of stands (dashed lines; data from Holmes *et al.* 1987). The upper three curves are for *A. saligna* and the lower four for *A. cyclops*.

seed decay was the result of germination and mortality (via pathogenic attack and physiological ageing). However, loss of viability through physiological ageing is considered to be much reduced in seeds with coat-imposed dormancy (Tran & Cavanagh 1984). The absence of density-dependent seed decay suggests that pathogenic attack on soil-stored *Acacia* seeds is minimal, unless pathogens attack only germinating seeds, in which case a density-dependent relationship would not be implicated. It further indicates the absence of any inhibitory effect on germination either via germinating seeds (cf. Inouye 1980) or dormant seeds (cf. Palmblad 1968; Linhart 1976).

Despite the high degree of hardseededness in the initial populations (75% in *A. cyclops* and 90% in *A. saligna*), 97% of the *A. cyclops* seeds and 45% of the *A. saligna* seeds either germinated or rotted in their first year of burial. Therefore the degree of hardseededness in a population may not be a reliable indicator of its longevity.

Other studies confirming low survivorship in *A. cyclops* soil-seed populations (Holmes 1988, in press) indicate that more seeds are lost through pre-emergence mortality than seedling emergence. Seeds of *A. cyclops* do not reach a peak germination percentage in laboratory trials, but continue to germinate over time: 32%

germination was attained by 60 days when the experiment was terminated (Jeffery *et al.* 1988). When seeds are stored in the laboratory, only 20–40% remain dormant after 1–2 years (Milton & Hall 1981). These studies suggest that the lens tissue in *A. cyclops* is readily broken down and that other factors, such as high soil temperatures (Gill 1985), may not be required to break dormancy.

Percentage dormancy in *A. saligna* is high until seeds are heated (Holmes 1988; Jeffery *et al.* 1988). However, this study indicates that loss of dormancy and/or pathogenic attack on seeds does occur, particularly in the first year. The degree of seed coat impermeability in legumes is related to the seed's moisture content and depends to some extent upon climatic conditions prevailing during late stages of maturation (Tran & Cavanagh 1984). The apparent lack of dormancy in the 1986 *A. saligna* seed population (Figure 1) may have resulted from moist atmospheric conditions prevailing between dehiscence and seed fall. Thus seed survivorship curves for different cohorts of *Acacia* seeds are unlikely to be identical.

In contrast to the constant death risk model (i.e. log-linear or Deevey Type II decline) (Roberts 1972; Harper 1977), seeds of both species which survived the first year had a greater probability of survival in their second year (Deevey Type III decline). Ralphs & Cronin (1987) found a similar pattern with locoweed seeds (*Astragalus lentiginosus*; Fabaceae) and attributed the large initial decrease in the population to the elimination of less hardy seed. As dormancy in *Acacia* is associated only with the seed coat and not the embryo (Cavanagh 1980), permeable and damaged seeds should be eliminated first, and the persisting population should be relatively more resistant to decay. The large seed banks measured under alien *Acacia* stands (Milton & Hall 1981; Holmes *et al.* 1987) may be the result of this persistent portion accumulating over many years. The log-linear decay model was developed primarily from studies of seed populations in annual weeds (Harper 1977), most of which do not have water-impermeable seed coats and may remain dormant in an imbibed state until exposed to light of the appropriate quality (Roberts 1972). Lonsdale (1988) argues that, in theory, seed longevity is unlikely to fit a log-linear model and should rather encompass all three basic survivorship models.

In conclusion, *Acacia* seed populations, especially those of *A. cyclops*, are rapidly depleted in the first year, but have enhanced survival probabilities with increasing time in the soil. Initial decay rates may be even higher when losses through predation are included. Comparison of results with published data on seed bank decline following felling indicates that longevity in seeds surviving their first 2 years of burial may be much higher than predicted by a log-linear decay model. Therefore complete elimination of Acacia seed banks may take many years, requiring a programme of periodic follow-up control (determined by the species' reproductive cycles) to ensure removal of these alien species from the vegetation.

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Effect of depth and duration of burial on alien *Acacia saligna* and *Acacia cyclops* seeds

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Abstract

Acacia seedling emergence, seed survival and decay at different soil depths were determined periodically over 30 months at a sandplain fynbos site. Seed fate was significantly different in the two species, with *A. saligna* having more persistent seeds. Most *A. saligna* seedlings emerged from 100 mm (23%) whereas in *A. cyclops* most emerged from 50 mm (60%), despite the latter's potential to emerge from greater depths. In both species, survival declined with depth of burial, but whereas few *A. cyclops* seeds survived at any depth, 75% of *A. saligna* seeds survived 30 months at 10 mm with predators excluded. Most seed germination and decay occurred during the first 6-12 months, indicating that the persisting population became relatively more hard-seeded. In the presence of seed predators (notably small mammals) survival of fresh seeds in the upper 50 mm of soil was minimal. As *A. cyclops* seed banks are predominantly transient, this species should be easier to control by felling than *A. saligna* which has persistent seed banks. It is recommended that in the latter species, burning may be required to kill the seeds. Alternatively, mechanically inverting the upper 150-200 mm of soil may reduce seed survival and seedling emergence.

Key words: decay, emergence, persistence, predation, water impermeable seed-coat dormancy

Introduction

Seed longevity in the soil is one important factor in assessing the seriousness of weed problems (Egley & Chandler 1978, Rolston 1978) and a knowledge of this, together with an understanding of factors that may control seed behaviour in the soil (notably dormancy) are an important part of improving current weed control practices (Zorner *et al.* 1984). Seed populations in the soil are reduced through predation, germination and death (including loss of viability, pathogenic invasion and pre-emergence mortality), the rates of which are affected by local environmental conditions (Weaver & Cavers 1979). In annual weeds, seed longevity is generally reported to increase with depth of burial (Roberts & Feast 1972; Cavers 1983; Zorner *et al.* 1984).

The highly successful invader species, *Acacia saligna* (Labill) Wendl. and *A. cyclops* A. Cunn ex G. Don, accummulate large, putatively long-lived, seed banks in the soil: 8 000 - 46 000 seeds.m^{-2} and 1 400 - 5 100 seeds.m^{-2} have been measured under dense stands of each species respectively (Holmes *et al.* 1987). These large seed banks are thought to be a major factor contributing to their success in South Africa (Dean *et al.* 1986) and to the difficulty experienced in their control (Milton & Hall 1981). If alien *Acacia* seeds escape pre- and post-dispersal seed predation, they may be incorporated into the soil via the activities of burrowing animals (Milton & Hall 1981). In sandy soils most *Acacia* seeds lie within the upper 80 mm, but some may be distributed to a depth of 350 mm (Milton & Hall 1981).

Acacia saligna and *A. cyclops* are "hard-seeded" species, i.e. their seeds have hard, water impermeable seed-coats (Rolston 1978). Hard-seededness is a physical exogenous form of innate dormancy (*sensu* Harper 1977) which protects the embryo from adverse environmental conditions and actively promotes seed longevity (Tran & Cavanagh 1984). Seed longevity in some Australian *Acacia* species may exceed 50 years (Cavanagh 1980). Maturing seeds must desiccate below a critical level before the seed-coat becomes

impermeable, therefore atmospheric conditions of high temperature and/or low Relative Humidity must prevail at seed maturation time (Rolston 1978). Above this critical level seeds may be conditionally "hard" but retain the ability to imbibe water (Rolston 1978). Once seeds have become impermeable, germination may only occur following abrasion of the testa. In *Acacia*, a small area of the seed-coat adjacent to the hilum, called the "lens", is thought to be the point of structural weakness which allows dormancy to be broken in hard seeds (Tran & Cavanagh 1984). To date, several studies indicate that *A. saligna* is more hard-seeded than *A. cyclops* (Milton & Hall 1981; Holmes 1988; Holmes 1989a) and therefore it would be predicted to have greater seed longevity, and lower seed germination and decay rates than *A. cyclops*.

In this study, *Acacia* seed germination, survival and decay at different soil depths were determined periodically over 30 months, in the absence of seed predators. Although seed longevity may be determined only from a much longer-term study, it may be inferred from survival rates of a fresh seed cohort buried in the soil (*cf.* Holmes 1989a).

Methods

The field experiment was done at the Pella Fynbos Biome Research Site ($31^{o}31'S$, $18^{o}32'E$), 62 km north-east of Cape Town. Pella has a Mediterranean, warm-temperate climate (Koppen's climatic type Cs) with over 70% of rainfall occurring from April - September (Jarman 1988). The area supports sandplain fynbos vegetation dominated by evergreen shrubs and Restionaceae, growing on acidic, sandy soil (Stock & Lewis 1986), which was five years old at the start of the experiment.

Ripe seeds were collected from dehisced pods on *Acacia saligna* and *A. cyclops* trees at Pella during December 1984 and January 1985, and sub-samples (n = 5 X 25 seeds) tested for germinability and viability as described below. Experimental design follows that of Weiss (1983). Bags of fibreglass

screening (1 mm^2 mesh) 250 mm deep, which were attached to 200 mm-diameter plastic rings, were filled with freshly sieved (2 mm^2 mesh) soil at the study site and buried in open spaces between fynbos plants, so that the ring was level with the soil surface. Fifty seeds of each species were sown in rows inside the bags at depths of 10, 50, 100 and 150 mm below the surface (one depth per bag) and then covered with the respective depth of sieved soil. The nearest *Acacia* trees were 50 m distant, thus new seeds were unlikely to fall into bags during trials. Provision was made for sampling 3, 6, 12, 18, 24 and 30 months after commencement, using a completely randomised block design with three replications. The trial was begun in January 1985, immediately following seed-fall in *A. saligna* and during the more protracted seed-fall in *A. cyclops*. However, within a week of placement, most 10 and 50 mm bags, and some 100 mm bags, had been disrupted by small mammals. Sieving the contents revealed that most of the seeds had been taken (Table 1). Disrupted bags were refilled and thenceforth protected from vertebrate predators by 15 mm^2 mesh wire exclosures.

Emerged seedlings were recorded each month, though more frequently during the first six months, and the seedlings removed. At each sampling time, bags were removed from the field, the contents sieved and seeds counted to determine numbers remaining at each depth. Any rotted seeds were also recorded. Surviving seeds were placed in 90-mm sterile, plastic petri dishes containing filter paper moistened with 6 ml benomyl solution [0,022% (m/v) active ingredient, *cf.* Clemens *et al.* 1977] and germinated in a controlled environment with a 12-h photoperiod at 25°C alternating with 20°C. Germinated seeds (as determined by >1 mm radicle extension) and rotted seeds were counted and removed over a period of four weeks. Remaining seeds were considered to be innately dormant and were manually chipped at the micropylar end and incubated for a further two weeks to determine their viability. As dormancy in *Acacia* is associated only with the seed-coat and not

Table 1. Mean percentage of seeds removed at each depth from bags disrupted by vertebrate seed predators during the first week of the field experiment, January 1985.

Depth buried (mm)	No. of bags disrupted (out of 18)	Mean % removed	
		A. saligna	*A. cyclops*
10	18	93,2	98,1
50	18	90,4	98,3
100	2	1	7
150	0	0	0

the embryo (Cavanagh 1980) a good estimate of viability should be obtained following abrasion of the seed-coat. Each sample could then be divided into five fractions: (1) emergent; (2) germinable (dormancy enforced e.g. by lack of available soil moisture); (3) innately dormant (non-germinable but viable fraction); (4) non-viable; and (5) missing (presumed rotted). Seedling emergence was used as a measure of germination in the field, although it underestimates it, especially at lower depths, owing to pre-emergence seedling mortality. The viable, persisting portions (2 + 3) were used as a measure of survival and the non-viable and missing portions (4 + 5) as a measure of decay.

In January 1986, another field trial was set up but with provision for only 12 months. Concurrently, a pot experiment using sieved field soil and one depth (50 mm), was commenced in order to compare the effect on the same cohort of seeds of continuous moisture *versus* field conditions. Counts of emerged seedings, sampling of bags and germination trials were carried out as described above. Potential depth of emergence was investigated in a second pot experiment: 100 seeds of each species were chipped at the micropylar end to break dormancy and placed at depths of 10, 50, 100, 150, and 200 mm in sieved field soil (50 of each species per pot). Pots were watered regularly to approximate conditions of field capacity and emerged seedlings were counted weekly.

Rainfall and evaporation data were obtained from the Weather Station at Pella. Counts of seedlings and seeds in each category were square-root transformed where required for the assumptions of normality and homogeneity of variances, and analysed by multiway analysis of variance (ANOVA) (Zar 1974). Where interactions were significant, the main individual effects were determined after removing the effect of the interaction by the classical regression approach. Tukey's Multiple Range Test (TMRT) (Zar 1974) was employed to test for differences among variable levels.

6

Results

Germinability and viability of seeds used in the 1985 field trial were, respectively: 10% ± 4 and 100% ± 0 (*A. saligna*) and 9% ± 7 and 84% ± 5 (*A. cyclops*) (mean ± S.D., n = 5 replicates of 25 seeds each). Equivalent values for the 1986 seed cohorts were 93% ± 3 and 100% ± 0 (*A. saligna*) and 10% ± 2 and 84% ± 5 (*A. cyclops*).

Seedling emergence

In *A. saligna*, seedling emergence from 10 and 50 mm depths over the first 12 months was correlated with mean daily rainfall and evaporation for the period preceding counts (Figures 1 & 2a; rainfall: $r = 0{,}54$, $P < 0{,}05$, $r = 0{,}82$, $P < 0{,}0005$; evaporation: $r = -0{,}63$, $P < 0{,}05$, $r = -0{,}66$, $P < 0{,}05$; for 10 and 50 mm depths, respectively). In *A. cyclops*, a similar pattern was found (Figures 1 & 2b) except that there was no significant correlation between emergence from 10 mm and rainfall (rainfall: $r = 0{,}38$, $P > 0{,}05$, $r = 0{,}50$, $P < 0{,}05$; evaporation: $r = -0{,}52$, $P < 0{,}05$, $r = -0{,}72$, $P < 0{,}005$; for 10 and 50 mm depths, respectively). There were no significant correlations between seedling emergence from 100 and 150 mm depths and either mean daily rainfall or evaporation during the periods preceding counts.

After 30 months in the soil, an average of 8%, 18%, 23% and 20% of *A. saligna* seeds compared to 29%, 60%, 27% and 10% of *A. cyclops* seeds had emerged as seedlings from sowing depths of 10, 50, 100 and 150 mm, respectively (Figure 2), with significant differences between the two species in relation to time and depth of emergence (ANOVA, $F = 6{,}7$, $P < 0{,}05$). Patterns of emergence for 1986 seed cohorts were similar to those for 1985, except that emergence was higher from most depths after 12 months (Figure 3).

In *A. saligna*, there was no overall effect of time on seedling emergence (ANOVA, $F = 1{,}46$, $P > 0{,}2$; Figure 4). Depth had a significant effect (ANOVA, $F = 15{,}7$, $P < 0{,}0001$), with greater emergence below than from 10

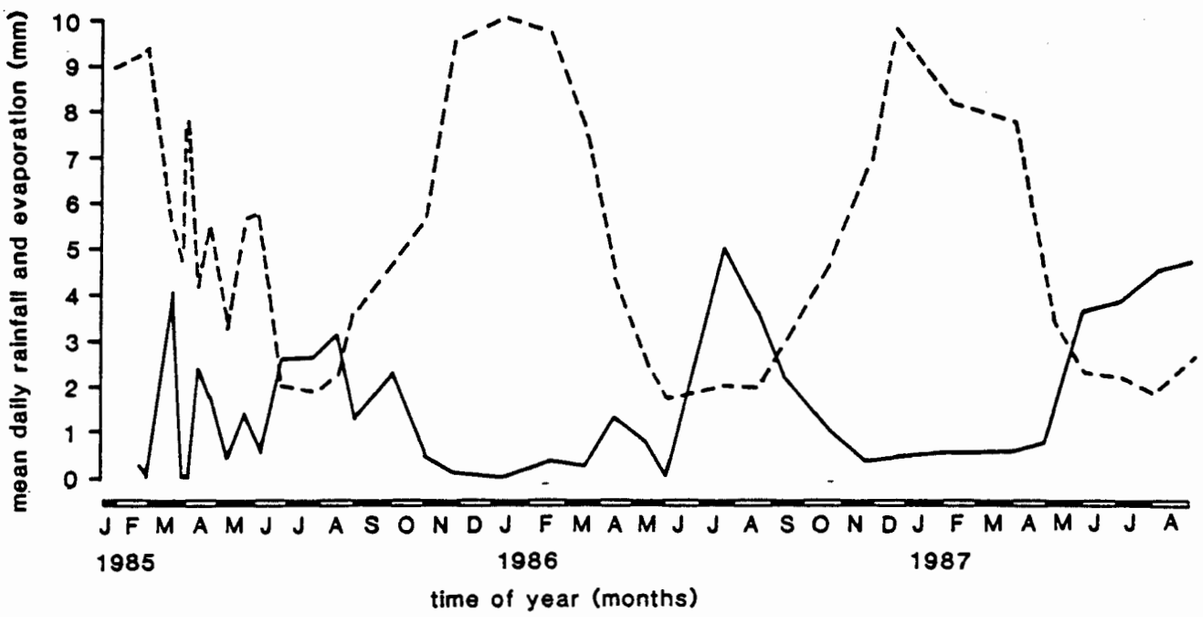

Fig. 1. Mean daily rainfall (solid line) and evaporation (dashed line) (mm) for the intervals between seedling counts at Pella. Data are from the Pella Weather Station.

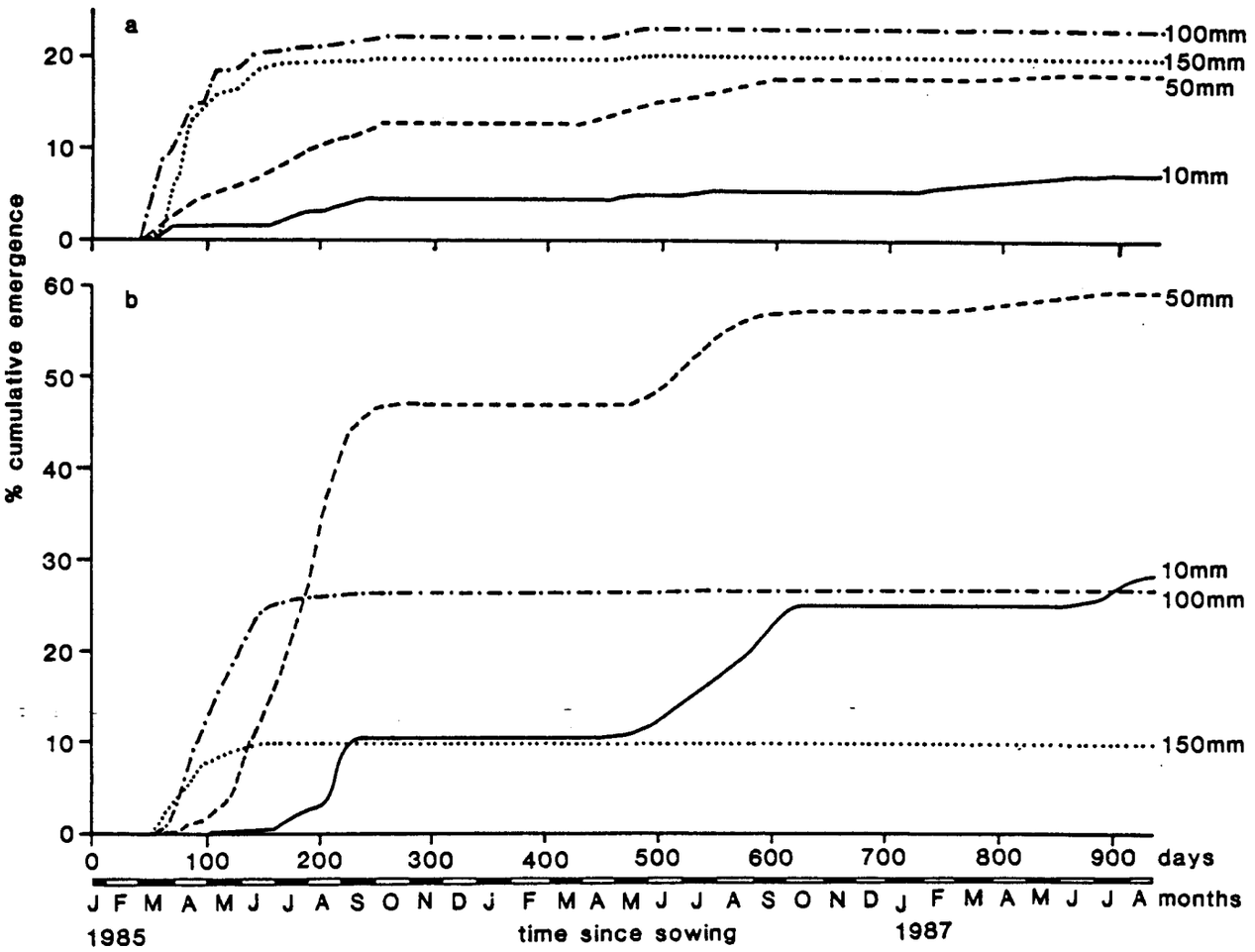

Fig. 2. Percentage cumulative seedling emergence (1985 seed cohort) in (a) *A. saligna* and (b) *A. cyclops* from 10, 50, 100 and 150 mm depths in the field.

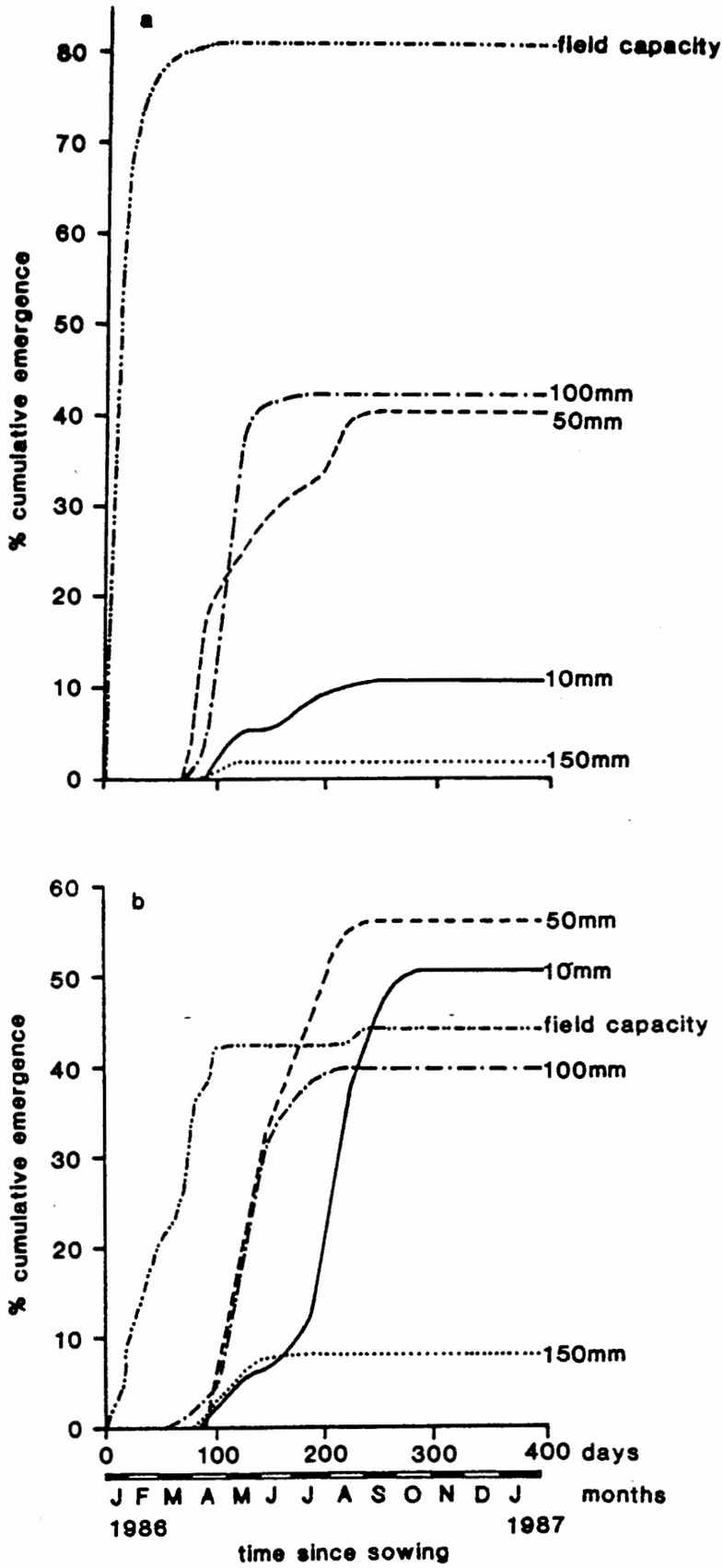

Fig. 3. Percentage cumulative seedling emergence (1986 seed cohort) in (a) *A. saligna* and (b) *A. cyclops* from 10, 50, 100 and 150 mm depths in the field, and 50 mm at field capacity in pots in the glasshouse.

mm depth (TMRT, P < 0,05). There was no overall effect of depth once the variation among blocks (ANOVA; depth X block, F = 2,83, P < 0,05) was taken into account. In *A. cyclops*, there was a significant interaction between time and depth (ANOVA, F = 3,0, P < 0,05; Figure 5), with no significant main effects after the interaction effect had been removed. Most emergence occurred during the first 12 months, after which there was little additional emergence (TMRT P < 0,05). More seedlings emerged from 50 and 100 mm than 10 and 150 mm depths (TMRT, P < 0,05), with greatest emergence from 50 mm.

Seeds buried at 50 mm in pots of moist soil in the glasshouse had a higher germination rate in both species, and in *A. saligna* greater seedling emergence than under field conditions (Figure 3). Following micropylar chipping, seedlings of *A. saligna* emerged successfully from depths of 10, 50 and 100 mm, but less successfully from 150 mm, whereas those of *A. cyclops* emerged successfully from all depths except 200 mm (Figure 5). *Acacia cyclops* seedlings succumbed to a damping-off fungus which lowered the final emergence percentages. Although *A. saligna* seedlings shared pots with *A. cyclops* seedlings, they were unaffected by the fungus.

Seed survival

Seed survival patterns differed significantly between species with respect to time and depth (ANOVA, F = 69,8, P < 0,0001; Figure 6). After 30 months of burial, an average of 75%, 73%, 49% and 9% of *A. saligna* seeds compared to 2,6%, 3,4%, 3,4% and 0,6% of *A. cyclops* seeds persisted at respective depths of 10, 50, 100 and 150 mm.

In *A. saligna*, there was a significant interaction between time and depth (ANOVA, F = 2,4, P < 0,05), with some significant variation among blocks (ANOVA, depth X block, F = 3,6, P < 0,05). Depth was the only main factor influencing seed survival after the interaction effects had been removed

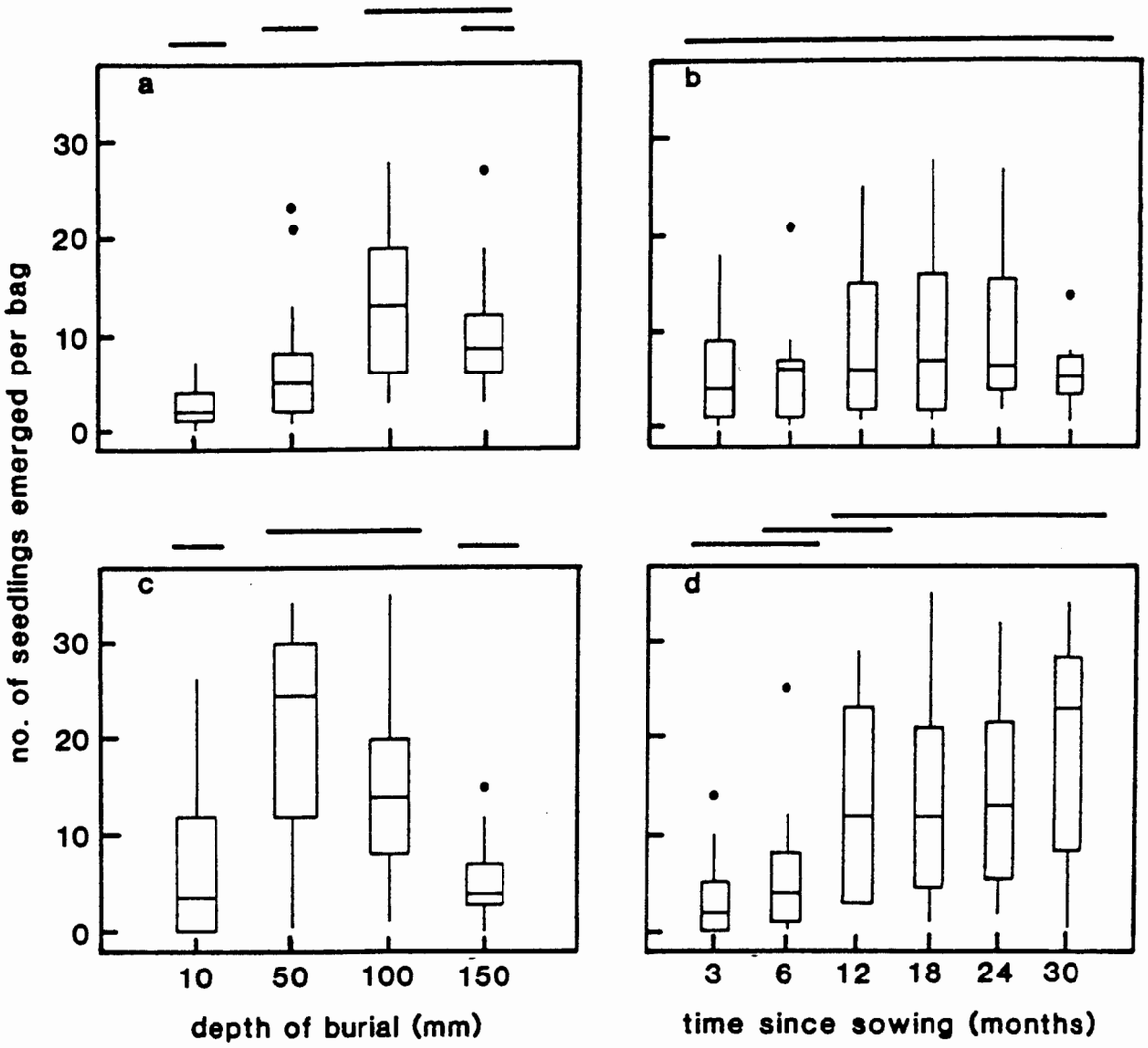

Fig. 4. Box and Whisker plots (Underhill 1981) of seedling emergence in (a,b) *A. saligna* and (c,d) *A. cyclops* from different depths (10, 50, 100 and 150 mm; n = 18) and at different time intervals (3, 6, 12, 18, 24 and 30 months; n = 12). Bars above figures represent the Tukey's Multiple Range Test: a bar continuing on one level indicates no significant difference among the encompassed groups ($P > 0.05$).

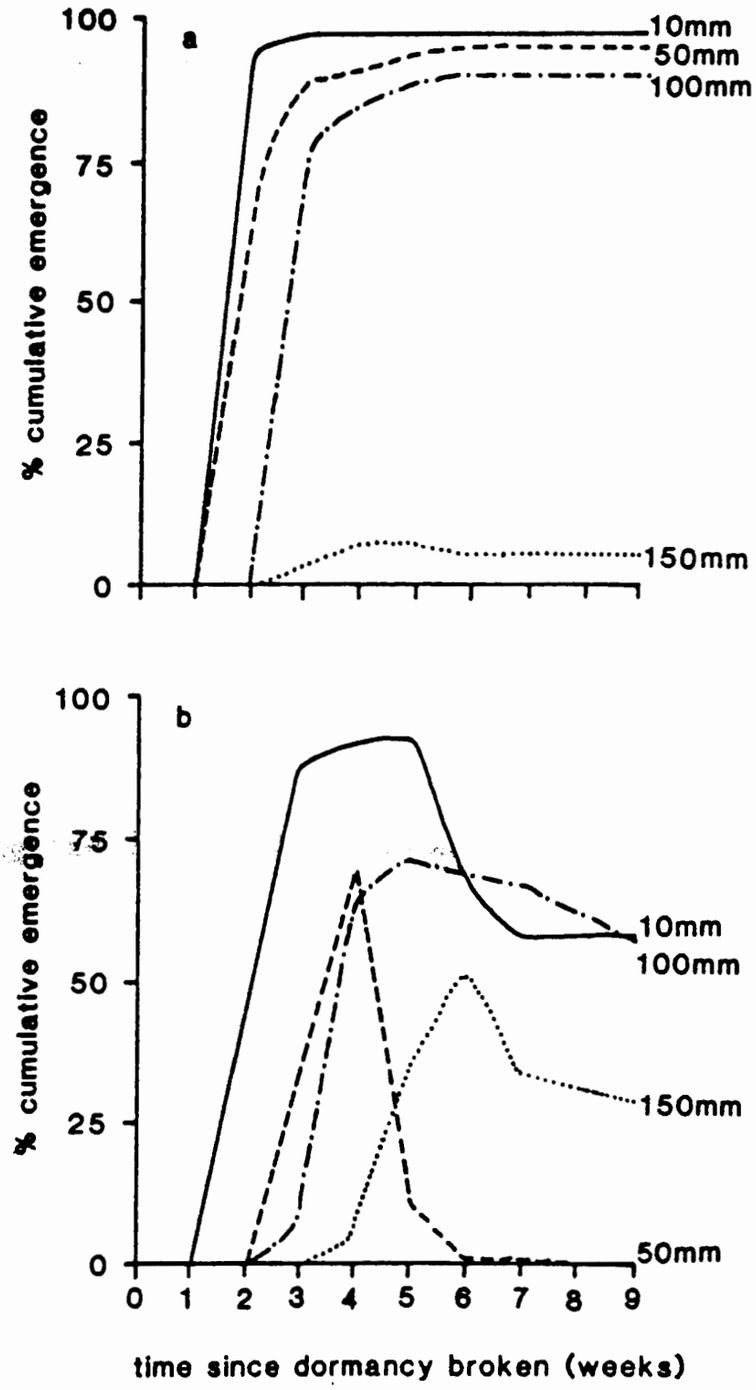

Figure 5. Percentage cumulative seedling survival (emergence minus mortality) from chipped seeds of (a) *A. saligna* and (b) *A. cyclops* from different depths in pots approximating field capacity in the glasshouse.

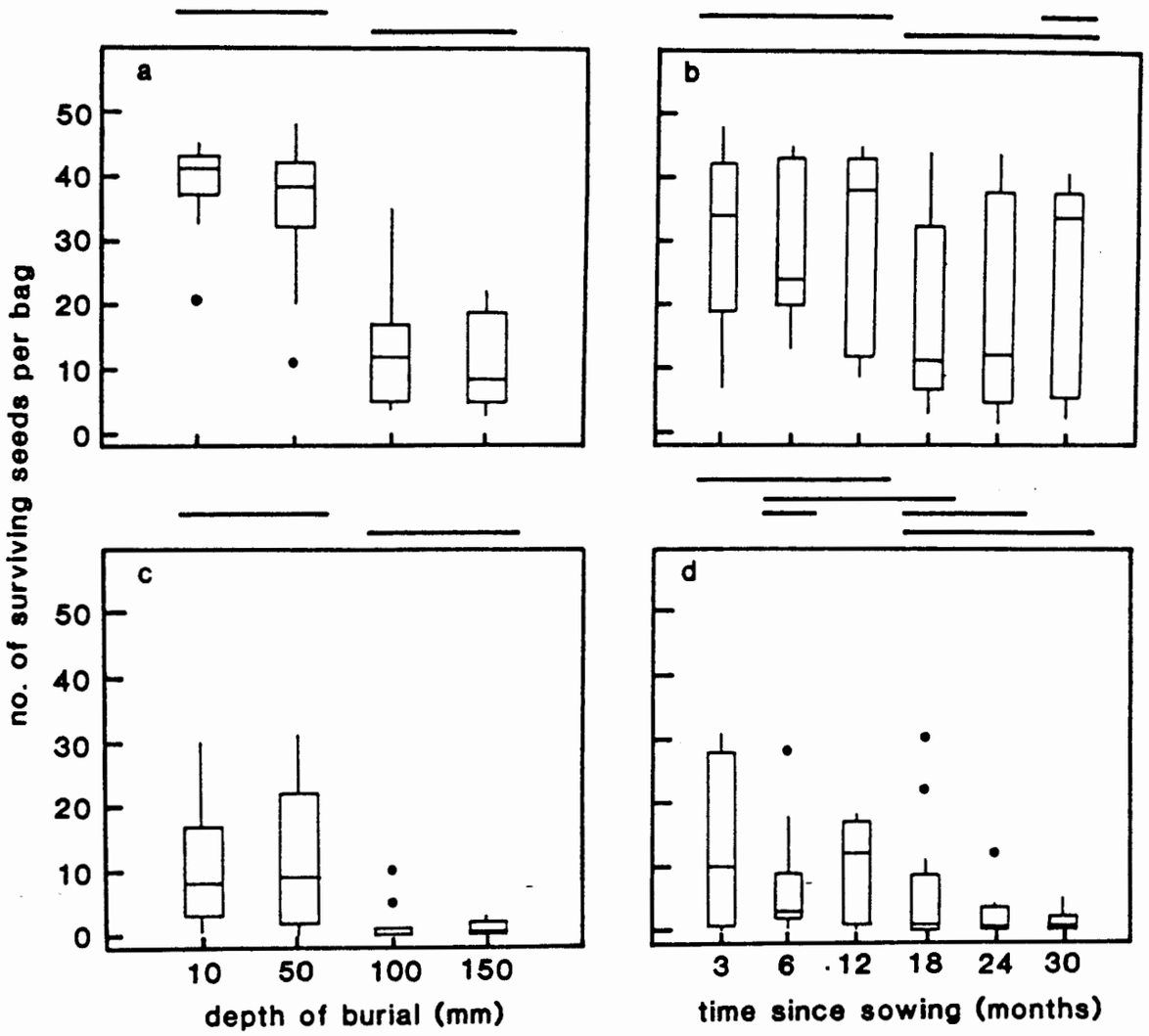

Fig. 6. Box and Whisker plots of seed longevity; legend as for Fig. 4.

(Classical Regression, depth: F = 5,51, P < 0,05), with survival higher at 10 and 50 mm than at 100 and 150 mm sowing depths (TMRT, P < 0,05). In *A. cyclops*, both time and depth had a significant effect on seed survival (ANOVA, time: F = 11,1, P < 0,0001; depth: F = 32,2, P < 0,0001), with some variation occurring among blocks (ANOVA, F = 7,2, P < 0,005). Seed survival declined with increasing time in the soil and was lower at 100 and 150 mm depths than at 10 and 50 mm depths (TMRT, P < 0,05).

A fraction of the persisting viable seeds were germinable (Figure 7). In *A. saligna*, both time and depth had a significant effect on the number of germinable seeds (ANOVA, time: F = 5,7, P < 0,005; depth: F = 4,9, P < 0,05). Seeds sampled in summer or autumn germinated more readily than those sampled in winter (TMRT, P < 0,05), and those sampled from 150 mm had more germinable seeds than those sampled from 10 mm (TMRT, P < 0,05). The latter effect was more evident if germinable seeds were expressed as a proportion of the total number of persisting viable seeds (Figure 7c). In *A. cyclops*, time and depth had a significant effect on the number of germinable seeds (ANOVA; time, F = 3,6, P < 0,05; depth, F = 3,3, P < 0,05), but too few seeds persisted after three months for meaningful interpretation, with no significant difference among subsequent sampling times (TMRT, P < 0,05).

Seed decay

The species difference in pattern of seed decay, with respect to time and depth, was highly significant (ANOVA, F = 141,4, P < 0,0001; Figure 8). After 30 months of burial, an average of 19%, 15%, 39% and 73% of *A. saligna* seeds compared to 59%, 33%, 55% and 91% of *A. cyclops* seeds decayed at respective depths of 10, 50, 100 and 150 mm.

In *A. saligna*, both time and depth had a significant effect on decay (ANOVA, time: F = 2,6, P < 0,05; depth: F = 45,1, P < 0,0001). However, with all depths combined, there was no difference among sampling times,

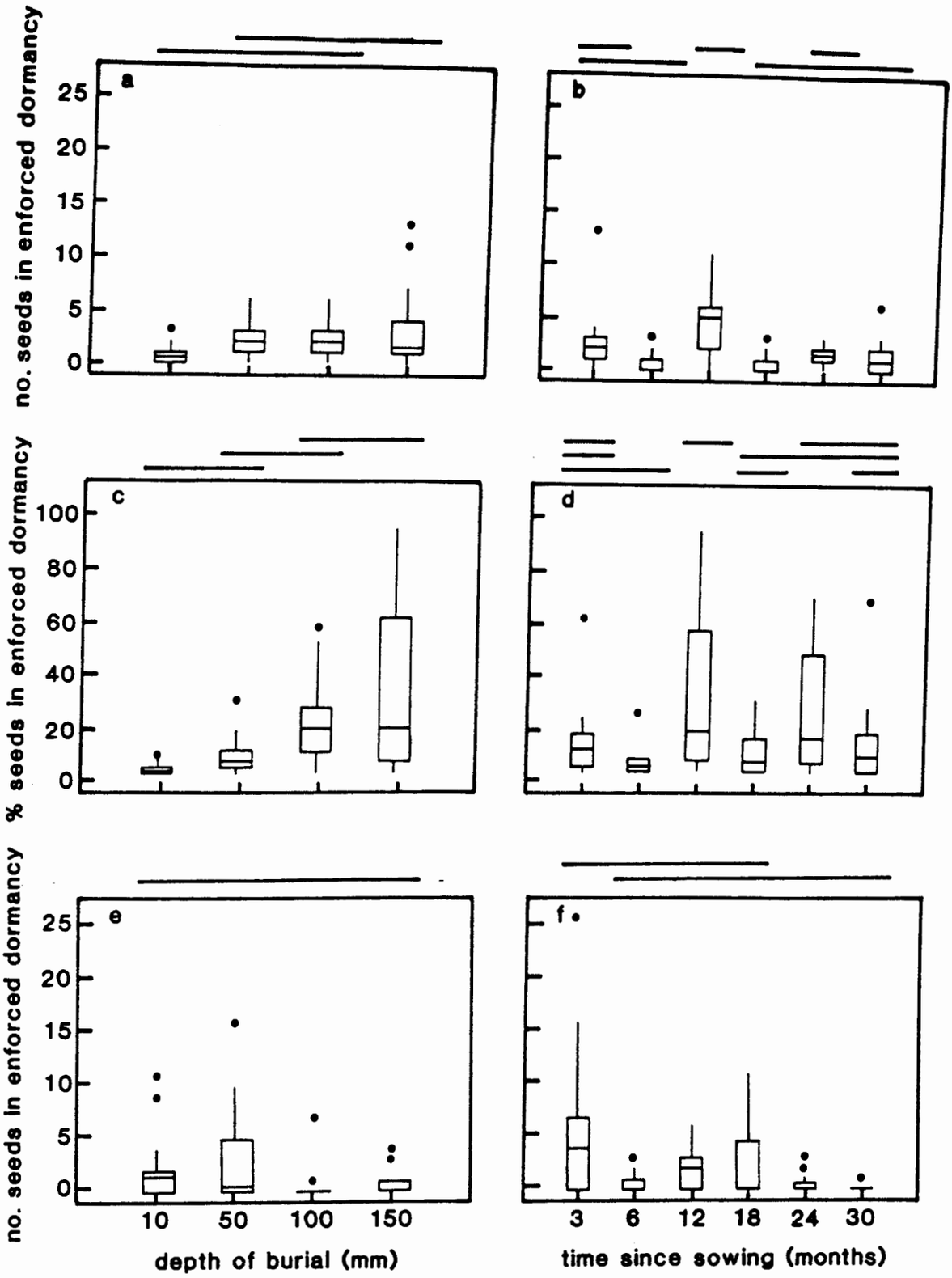

Fig. 7. Box and Whisker plots of germinability; legend as for Fig. 4., except (c,d) germinability in *A. saligna* as a proportion of the persisting seed population, and (e,f) germinability in *A. cyclops* .

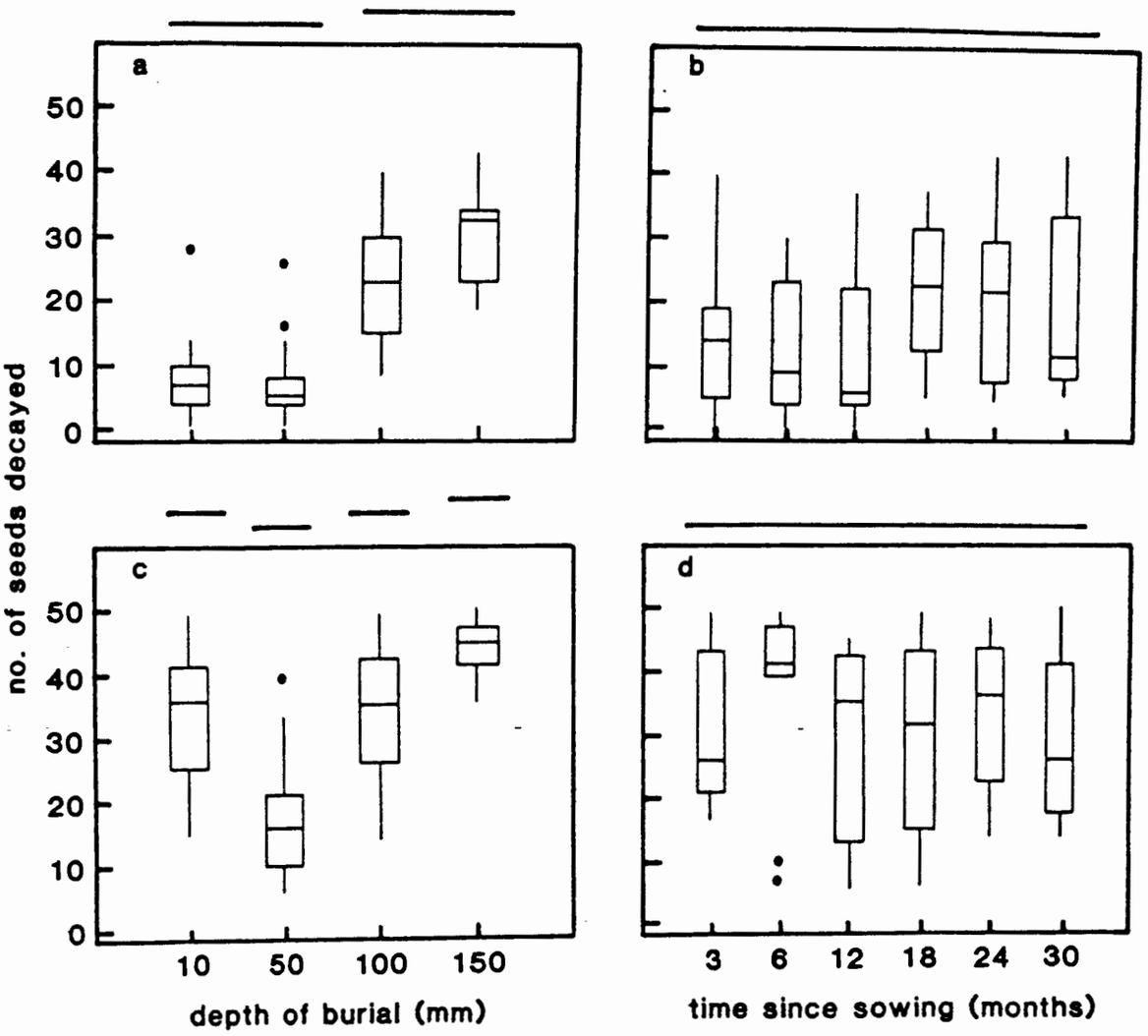

Fig. 8. Box and Whisker plots of seed decay; legend as for Fig. 4.

whereas fewer seeds at 10 and 50 mm depths decayed than at 100 and 150 mm depths (TMRT, $P < 0.05$). In *A. cyclops*, only depth affected seed decay (ANOVA, $F = 32,5$, $P < 0,0001$), with the least decay occurring at 50 mm depth increasing to highest at 150 mm (TMRT, $P < 0,05$).

Discussion

Despite initially high levels of water impermeable dormancy and viability, a large proportion of seeds in both species either germinated or decayed during the trials, the rates of these processes depending upon burial depth (see Figure 9 for summary of results). As the number of emergents often exceeded the number of germinable seeds in the initial population, water impermeable dormancy must be overcome in the soil, possibly as a result of diurnal temperature fluctuations near the soil surface or the action of soil bacteria on the lens tissue (Tran & Cavanagh 1984).

Following burial, *A. cyclops* seeds readily lose water impermeable dormancy, whereas *A. saligna* seeds retain dormancy and have potentially low germination and decay rates and high longevity, as predicted. However, at depths below 50 mm, survival in *A. saligna* seeds was low, both as a result of increased germination and decay, and indicates for this species that water impermeable dormancy is more readily broken in moist than dry soil. Two further results may corroborate this finding: at the drier depths of 10 and 50 mm, seedling emergence was correlated with rainfall in the preceeding month; and faster germination occurred in watered pots than in the field. Possibly certain scarification processes (e.g. microbial action) operate only in moist soil. That a greater proportion of the persisting *A. saligna* seed population was germinable when sampled in summer or autumn than in winter, suggests that water impermeable dormancy was broken prior to the onset of summer drought with those seeds remaining in enforced dormancy until onset of the winter rains.

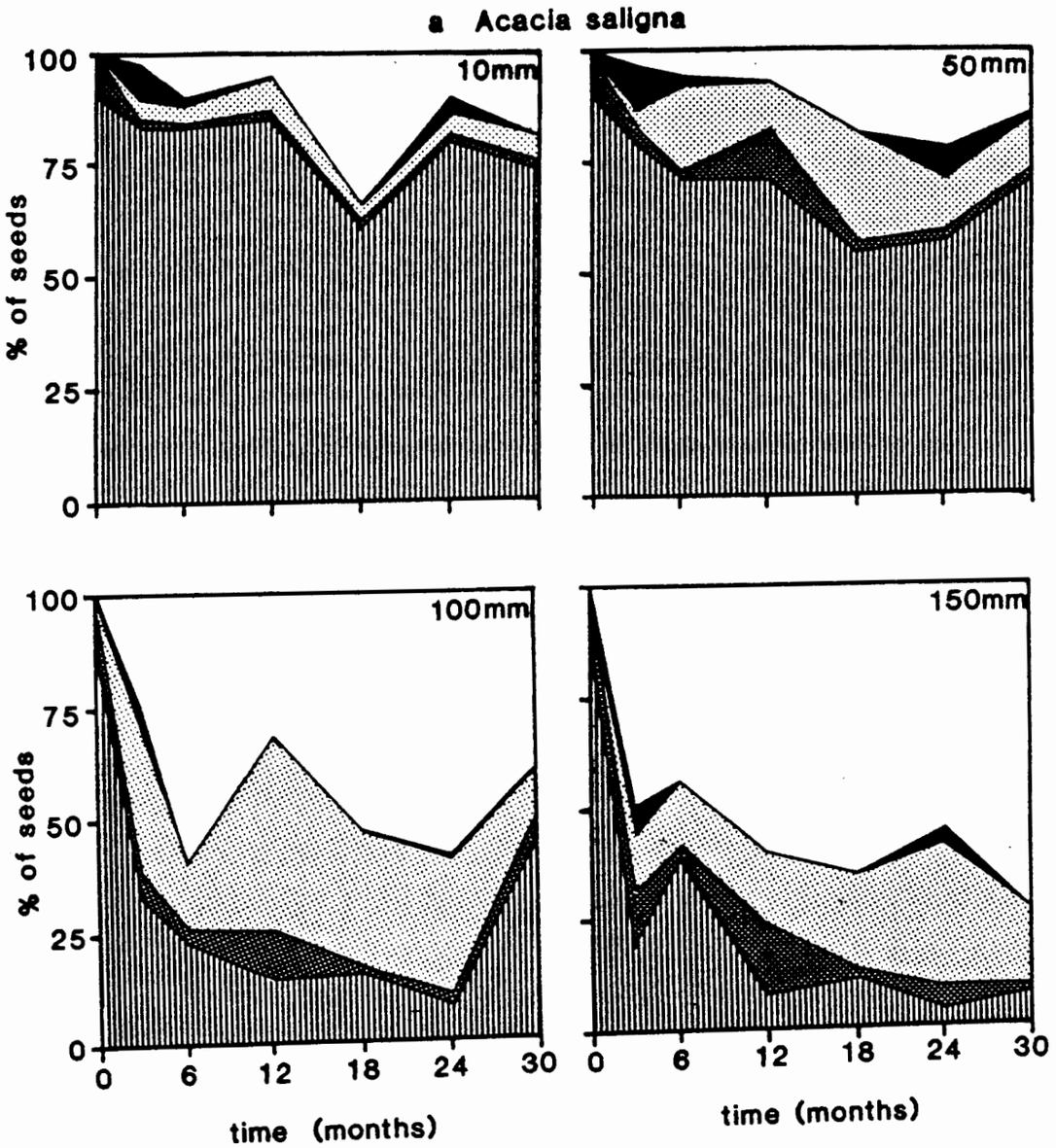

Fig. 9. Summary of the fates of a) *A. saligna* and b) *A. cyclops* seeds buried at four different depths in the soil over a 30 month period. Missing = white, dead = black, emerged = stippled, dormancy enforced = shaded, dormancy innate = striped.

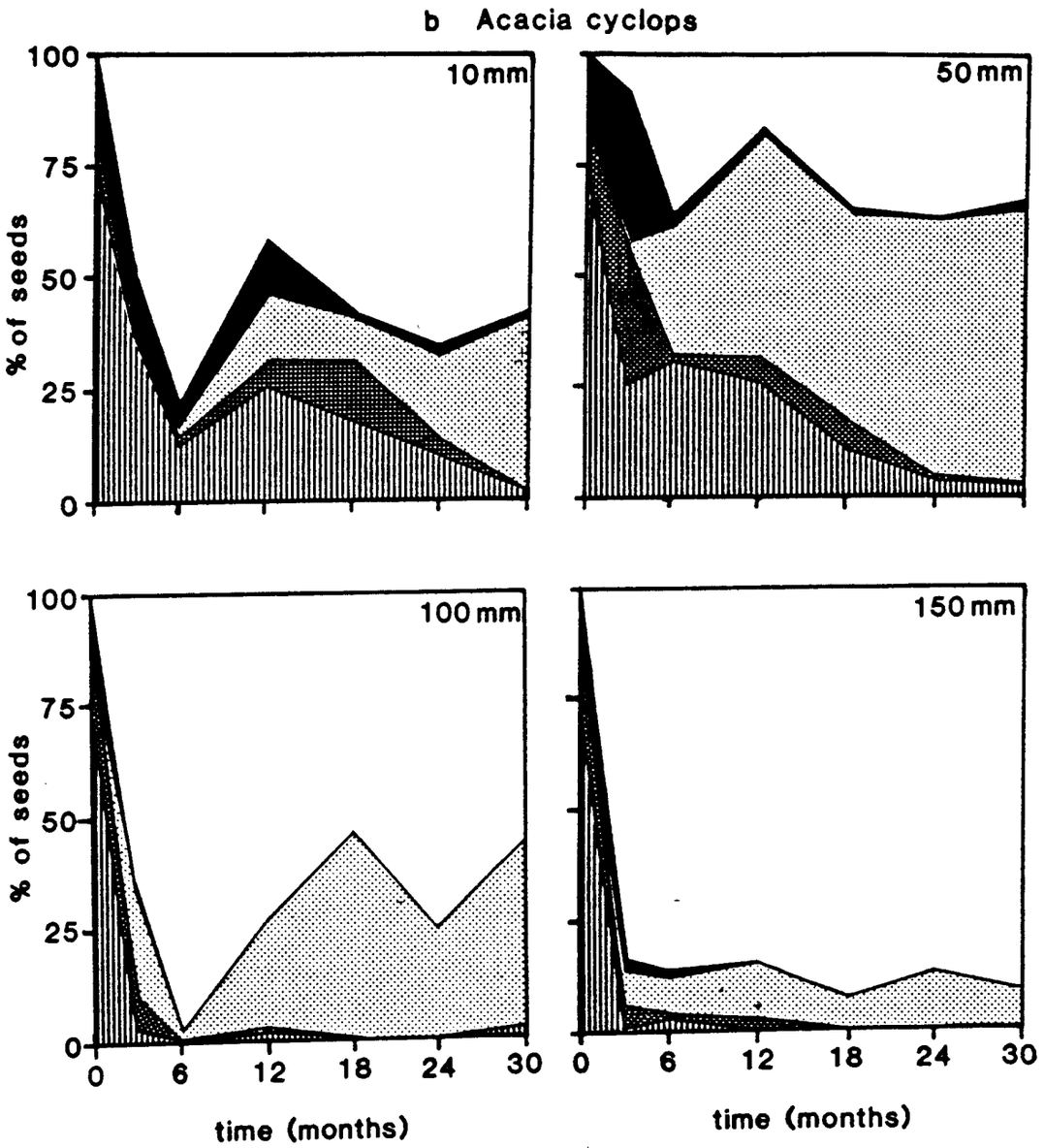

Fig. 9. Summary of the fates of a) *A. saligna* and b) *A. cyclops* seeds buried at four different depths in the soil over a 30 month period. Missing = white, dead = black, emerged = stippled, dormancy enforced = shaded, dormancy innate = striped.

In contrast to the results of other studies on weed seed behaviour in which burial depressed germination and enhanced survival (Roberts & Feast 1972; Stoller & Wax 1974; Zorner *et al.* 1984; Lonsdale *et al.* 1988), *Acacia* seed survival declined with increasing depth of burial. This highlights the importance of dormancy in determining weed seed behaviour, as few weeds of cultivated soils are hard-seeded (Roberts & Feast 1972) and rely on other forms of innate or induced dormancy for survival.

That most germination and decay in *A. saligna* occurred during the first three months, with little thereafter, indicates that the less hardy seeds are eliminated first and the persisting population is relatively more resistant to decay (cf. Ralphs & Cronin 1987 for locoweed seeds). In *A. cyclops*, germination continued throughout the first 12 months, after which only a small proportion of the population persisted. As noted previously (Holmes 1989a) the pattern of decline in *Acacia* seed banks does not conform well to the log-linear or Deevey Type II model which was derived from studies of annual weed seeds (Roberts 1972; Harper 1977).

Despite their larger size (33 versus 16 mg) and potential to emerge from greater depths, seeds of *A. cyclops* emerged best from a shallower depth than those of *A. saligna*. A high proportion of *A. cyclops* seedlings may emerge in the field, but this species is susceptible to pre-emergence mortality probably owing to seed-rotting (Harper 1977) if conditions for germination are sub-optimal.

In contrast to the 1985 *A. saligna* seed cohort which was predominantly hard, the 1986 *A. saligna* cohort was conditionally hard but germinated readily when moistened. Possibly the conditions under which the 1986 seeds matured prevented sufficient seed desiccation. Thus, as has been noted for other species (Roberts & Feast 1972), no two seed cohorts are identical and some cohorts will contribute more to the persistent seed bank than others. Post-dehiscence desiccation, leading to increased hard-seededness, may occur, as fewer seedlings emerged following shallow burial than germinated in the initial trials.

Without vertebrate exclosures, survival of fresh seeds at and above 50 mm was minimal, emphasizing the importance of deep burial to seed longevity in fynbos vegetation (Bond & Breytenbach 1985). This raises the question of how acacias have been able to invade fynbos communities with apparent ease. It is possible that ants bury alien *Acacia* seeds, thus protecting them from predation and enhancing their survival (Holmes 1989b).

In conclusion, seed bank turn-over in *A. saligna* is slow, promoting rapid seed accumulation under dense stands. By contrast, seed banks of *A. cyclops* accumulate gradually and in most cases will be composed predominantly of the current year's crop. Thus *A. saligna* seed banks conform to the 'Type IV' persistent seed bank model of Thompson & Grime (1979), which confers potential for regeneration in unpredictably disturbed habitats; in this instance habitats adapted to fire. As *A. cyclops* has a small proportion of seeds which persist for over a year, it conforms best to the 'Type III' model which has characteristics intermediate between those of transient and persistent seed banks. Thus *A. cyclops* may exploit seasonally disturbed habitats (e.g. coastal dunes) as well as the more unpredictably disturbed habitats. As *A. cyclops* seed banks are fairly transient, this species should be easier to control than *A. saligna*. In the latter, clearing methods which incorporate burning will be necessary to kill a large porportion of the seeds. Alternatively, mechanically inverting the upper 150-200 mm of soil (assuming that the seed bank is concentrated near to the surface) would greatly reduce seed survival and seedling emergence in this species.

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Holmes

Vertical movement of soil-stored seeds at a sandplain fynbos site

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Abstract

Vertical movement of *Acacia* seeds placed at the soil surface and at various depths in the soil profile was investigated over one year at a sandplain fynbos site. Both upward and downward movement of seeds occurred, but significantly more seeds were displaced in profiles disturbed by molerat mound production than in undisturbed profiles. For seeds originally placed at the surface, only 3% of those recovered were incorporated into the soil after one year. In disturbed profiles, more seeds moved up than down, with seeds exhumed to the surface, in contrast to undisturbed profiles in which upward movement was negligible. Where burrowing animals are absent, seeds tend to be concentrated more towards the soil surface than in areas where they are present. In deep sandy soils, burrowing rodents are important agents both in seed burial and in exhuming buried seeds to the surface.

Key words: molerats, mound production, seed burial

Introduction

Vertical movement of seeds in the soil is assumed to occur via the burrowing and seed-caching activities of animals, in percolating rain water, and down wetting and drying fractures or decomposed root channels (Harper 1977). In the fynbos biome, South Africa, about 20% of plant species are thought to be myrmecochorous and their seeds are commonly buried 40-70 mm below the soil surface in ant nests (Bond & Slingsby 1983). Although there are no seed-caching rodents in the region (Slingsby & Bond 1985), several species create extensive burrow systems, especially in lowland ecosystems (Smithers 1983).

This study was undertaken as part of a broader investigation of alien *Acacia* seed bank dynamics. Soil-stored seed banks of *Acacia* species may have a depth distribution of up to 0,35 m in sandy soils, although seeds are most concentrated in the upper 80 mm (Milton & Hall 1981). *Acacia* seeds have water impermeable dormancy (Rolston 1978) and may remain dormant for many years (Cavanagh 1980). It is relevant to know how quickly seeds may be incorporated into the soil profile as seed longevity and seedling emergence may change with depth of burial (Roberts & Feast 1972). Whether buried seeds can be exhumed to the surface might become a critical factor in situations where the upper portion of the seed bank is eliminated, for example by fire (Holmes 1989a). This study was run concurrently with another on the effect of depth and duration of burial on *Acacia* seed germination, survival and decay (Holmes 1989b). This study investigates whether there is significant upward and downward movement of seeds in the soil profile and whether seeds may be exhumed to the soil surface.

Methods

An area of level terrain in young sandplain fynbos vegetation (burnt five years previously) at Pella ($31^{o}31'S,18^{o}32'E$) was chosen for the study. The soil is a deep acidic sand of the Clovelly form (Stock & Lewis 1986) and the

area experiences a Mediterranean, warm-temperate climate with over 70% of rainfall occurring from April - September (Jarman 1988). Burrowing rodents which may occur in the region are the Cape dune molerat (*Bathyergus suillus* (Schreber)), Cape molerat (*Georychus capensis* (Pallas)), common molerat (*Cryptomys hottentotus* (Lesson)) and Cape gerbil (*Tatera afra* (Gray)) (Smithers 1983). The striped fieldmouse (*Rhabdomys pumilio* (Sparrman)), which also occurs in the region, may sometimes burrow to a depth of 0,5 m (Smithers 1983). Density figures are available only for *B. suillus*, which averages 0,9 individuals per hectare at Pella (Davies & Jarvis 1986).

In March 1985, fifteen pits were excavated in open spaces between plants to a depth of about 0,3 m and one face cut to vertical. Using a narrow corer (10 mm diameter by 0,3 m long), which had most of its upper surface removed, horizontal cores (maintained by spirit level) were removed from the profile behind the vertical face in a four by five grid. The four rows were positioned at 30, 60, 100 and 170 mm below the soil surface (Figure 1) and the five columns were spaced 50 mm apart. After removing each soil core, six colour-tagged seeds were evenly spaced on the corer and inserted into the hole. In this way, 30 seeds were placed at each depth. Pits were refilled with soil to prevent collapse of the profiles and 30 additional seeds placed onto surfaces of the profiles and lightly covered with soil. Finally 15-mm mesh wire exclosures were pegged over the profiles to minimize above-ground interference and to mark their positions.

Acacia saligna (Labill.) Wendl. seeds gathered from the litter layer of a dense *Acacia* stand were used in the study. The seeds were a minimum of one-year-old and had lost their elaiosomes. Before burial, seeds were coated with one of five colours of enamel paint (one colour per depth).

A year later in either March (n = 10) or July (n = 5), profiles were excavated to determine seed positions. An aluminium frame (0,5 X 0,5 m)

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A year later in either March (n = 10) or July (n = 5), profiles were excavated to determine seed positions. An aluminium frame (0,5 X 0,5 m)

with a 40 mm-deep edge was placed around the profile and the soil within the frame excavated carefully in 10 mm spits. Soil was removed to a depth of 200 mm and sieved to extract seeds.

To correct for possible excavation error, seeds were assumed to have moved in the profile only if they were vertically displaced by 30 mm or more. Mean numbers of seeds displaced ± S.D. were calculated from the 15 profiles and also separately for those profiles disturbed (n=7) and undisturbed (n=8) by molerat mound production. Differences between upward and downward movement of seeds and movement of seeds placed at different depths were tested by the Mann-Whitney U Test (Siegel 1956).

Results & Discussion

Out of 150 seeds placed in each profile, 93,1 ± 20,7 (mean ± S.D., n=15) were recovered a year later. On average, more seeds were lost from the surface than from any other depth (74% *versus* 29%), indicating that despite a coating of enamel paint, exposure to sunlight and/or small predators greatly reduced longevity.

Overall, 9,1 ± 14,7 seeds, equivalent to 10% of recovered seeds, moved up the profile by 30 mm or more, compared to 5,6 ± 7,7, equivalent to 6%, which moved down the profile, with no significant difference between upward and downward movement (U test, P>0,05). For seeds originally placed at the surface, only 0,2 ± 0,6, equivalent to 3% of recovered seeds, were incorporated into the soil after one year. However, seven of the profiles had been disturbed by *B. suillus* mound production and in those profiles significantly more vertical displacement of seeds occurred than in undisturbed profiles (U test, P<0,005): 25,7 ± 14,6, equivalent to 26% of recovered seeds, compared to 5,1 ± 5,1, equivalent to 6% of recovered seeds, were displaced, respectively (Table 1). The mound was treated as a separate

Table 1. Vertical movement of *Acacia* seeds (X ± SD) after one year in a sandy soil profile

Initial seed depth (mm)	No. seeds recovered	Vertical movement ≥30 mm Up	Down
Profiles disturbed by molerats (n=7)			
0	6.86±7.10	–	0.43±0.79
30	25.86±4.06	2.57±4.76	2.71±4.35
60	20.86±8.67	1.86±3.67	1.00±1.73
100	22.86±5.21	8.14±8.43	2.29±5.19
170	23.00±4.04	6.71±7.06	–
Profiles undisturbed by molerats (n=8)			
0	8.62±7.23	–	0.00±0.00
30	23.75±4.59	0.00±0.00	2.25±2.60
60	13.25±8.63	0.00±0.00	1.00±1.60
100	18.88±6.20	0.12±0.35	1.62±2.07
170	22.75±3.20	0.12±0.35	–

soil layer and seeds buried under mounds were not considered to have moved down the profile unless they were displaced from their original level.

In molerat-disturbed profiles, more seeds moved up than down (U test, $P < 0,05$), in contrast to undisturbed profiles in which more seeds moved down than up (U test, $P < 0,01$) (Table 1). Furthermore, in disturbed profiles, upward movement of seeds was more pronounced in lower (100-170 mm) than in upper (0-60 mm) strata (U test, $P < 0,05$), whereas there was no depth differentiation in undisturbed profiles or for downward movement of seeds.

Although seeds are pushed to the soil surface as *B. suillus* expels soil from burrows, the long-term effect of burrowing and mound production will be a lowering of the soil profile and a deposition of soil on the surface, which will simultaneously bury seeds lying in the litter layer. Estimates from another study (Jarvis *et al.* 1985) indicate that in young fynbos 2% of the surface is covered by mounds annually, with complete turn-over of the surface soil occurring after approximately 50 years. Using mound volume figures it would take only an estimated nine years for the ground surface to be covered (on average) by a new layer of soil 10 mm thick. The greater upward movement of seeds from lower strata may relate to either moister soil conditions at those depths, or the shallower angle of the burrow intercepting more seeds lower down the profile compared to near the surface, where the burrow becomes vertical.

As *B. suillus* burrows are located at depths below most seed banks (>0,4 m) (Davies & Jarvis 1986), the burrowing *per se* is unlikely to relocate seeds. However, in some soils, molerats may burrow at shallower depths to feed (Jarvis *et al.* 1985); and in more consolidated soils *C. hottentotus*, with its shallower burrow systems (<0,35 m), predominates (Davies & Jarvis 1986). No information is available on the burrowing activities of *G. capensis*, *T. afra* or *R. pumilio*.

Even in the absence of obvious disturbance by molerats, significant vertical movement of soil-stored seeds occurred. But whereas a large proportion of deeply buried seeds may be brought to the surface by molerat excavations, the probability of seeds being exhumed in the absence of such mound production is very low. The predominantly downward movement in undisturbed profiles may be the result of seeds falling down small invertebrate burrows or holes left by decaying plant roots. These processes may have been facilitated by the action of percolating rain water. Examples of seed movement attained after one year in a disturbed and undisturbed profile are shown in Figure 1.

Thus in sand plain fynbos vegetation burrowing rodents play a significant role in the dynamics of soil-stored seeds, both in exhuming buried seeds and in burying surface seeds. At the same site, percentage seed germination at or near the soil surface was low, with optimum depths for seedling emergence being 100 mm (*A. saligna*) and 50 mm (*A. cyclops* A. Cunn ex G. Don), and seed survival below 100 mm was minimal (Holmes 1989b). Thus whereas shallow burial may protect *Acacia* seeds from predation, deep burial lowers their survival probability. The extent to which rodents persist in *Acacia*-infested vegetation is not known, but the elimination of most other plant species as stands become dense is likely to reduce significantly the number of rodents and therefore their burial action.

Indigenous ants may not contribute to deep burial of seeds (Bond & Slingsby 1983), but they have been shown to remove significant quantities of *A. cyclops* and *A. saligna* seeds from the soil surface (Holmes 1989b) and may therefore be important in the shallow burial of these seeds.

Many areas originally planted with acacias were non-vegetated dunes (Shaughnessy 1986), which may also have been devoid of ants and burrowing rodents. One would therefore predict that seed banks would be concentrated more towards the soil surface in such areas than in areas of fynbos-invaded

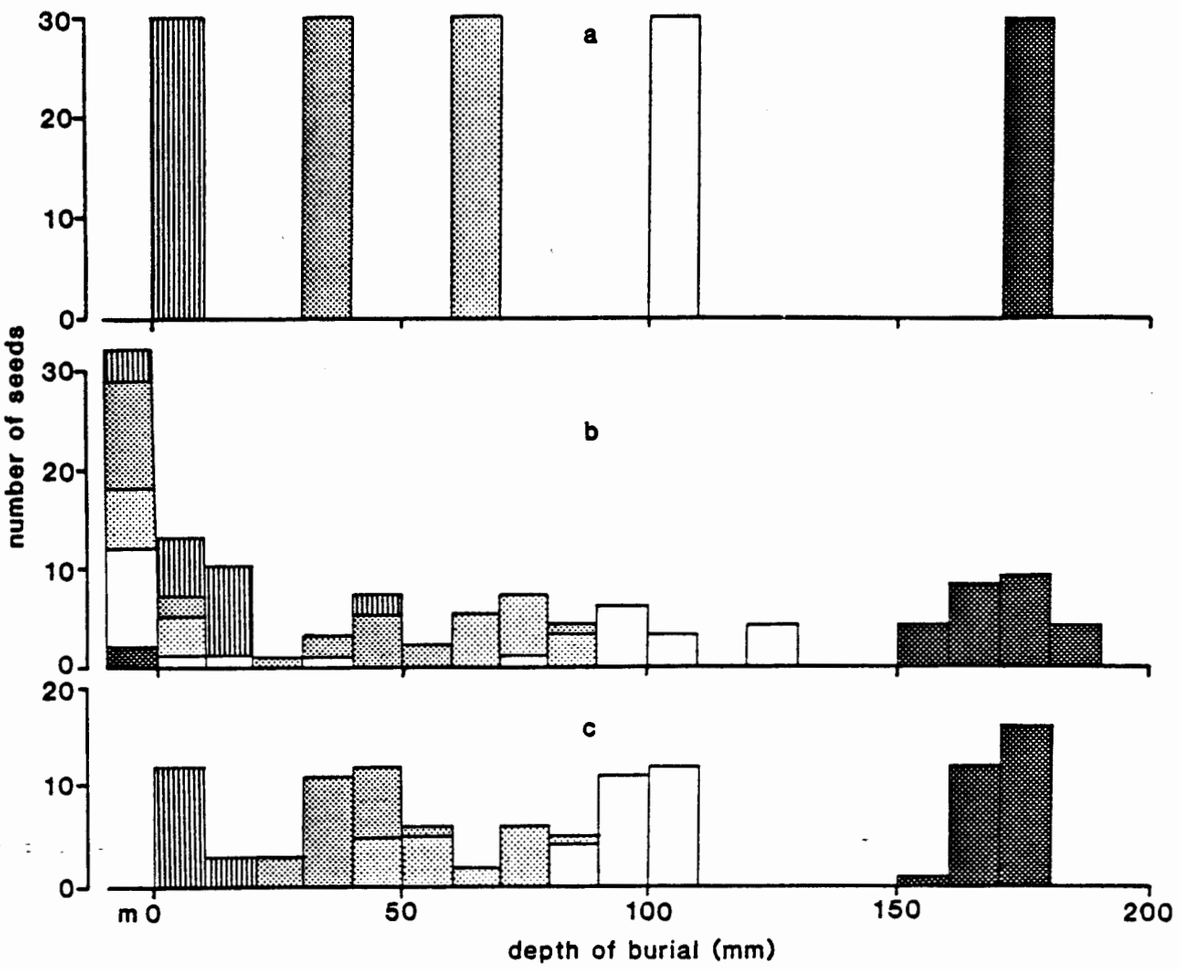

Fig. 1. Distribution of tagged seeds in the soil (a) at the start of the experiment, and after one year in a profile (b) disturbed by molerat mound production, and (c) undisturbed by molerat mound production; m = mound.

vegetation. Wind-blown sand may be important in burying seeds in dunefield areas, especially in areas of low vegetation cover, but this remains to be investigated. A preliminary investigation of the vertical distribution of *Acacia* seeds in dense stands supports the above prediction (Figure 2), and further indicates that in previously non-vegetated areas seeds are more likely to remain in the litter layer than to be incorporated into the mineral soil. An important implication of this is that burning treatments should eliminate a larger proportion of the *Acacia* seed bank at bare-dune compared to fynbos-invaded sites.

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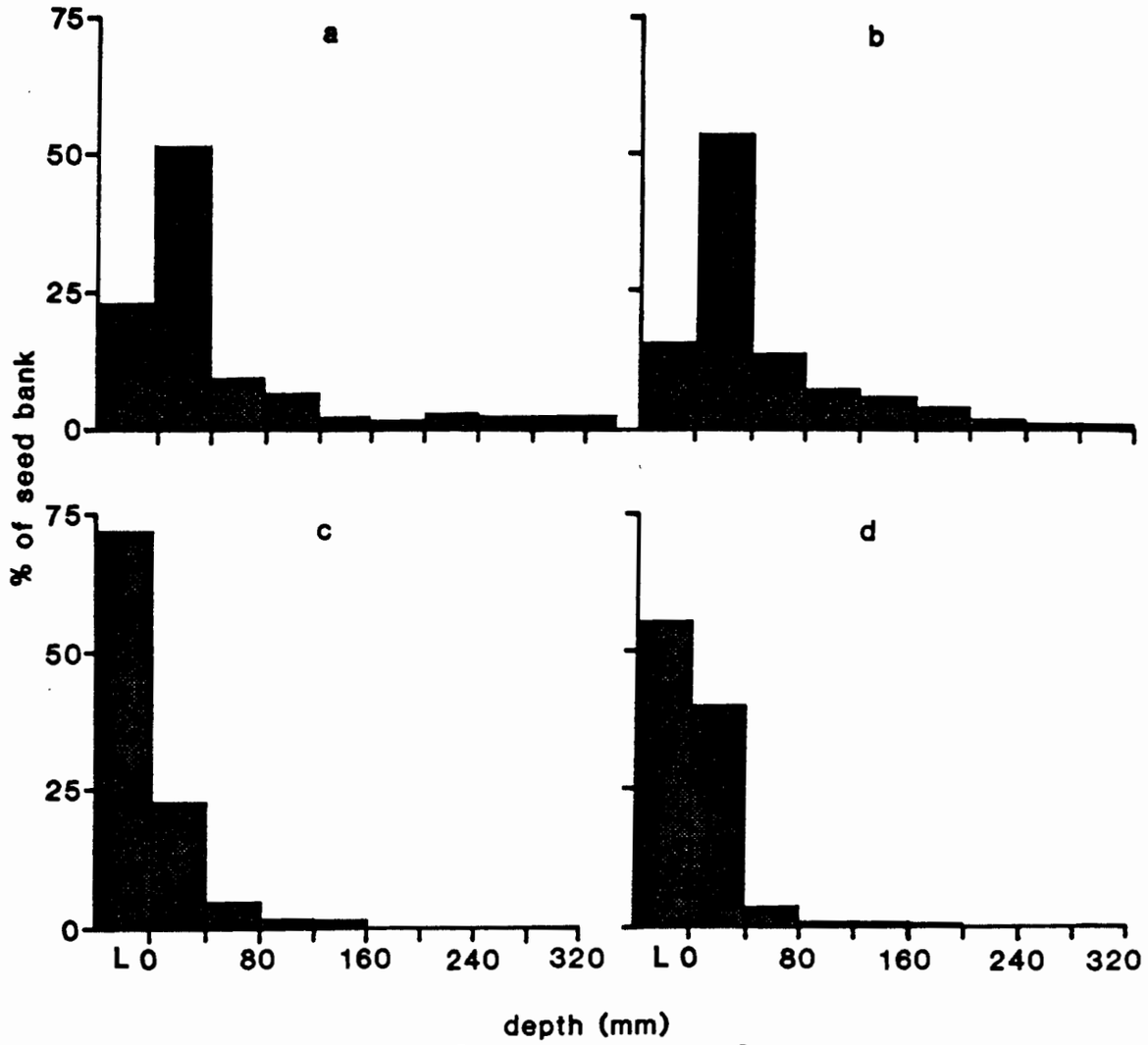

Fig. 2. Vertical distribution of seeds in sandy soils under dense *Acacia* stands: (a), (b) areas of previous fynbos vegetation; (c), (d) areas previously non-vegetated. (a) *Acacia saligna*, Penhill (data from Milton & Hall 1981); (b) *A. saligna*, Pella; (c) *A. cyclops*, Goukamma Nature Reserve; (d) *A. cyclops*, Walker Bay Forest reserve; L = litter.

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III SYNTHESIS

(Numbers in parentheses refer to relevant papers)

(a) **Summary of Research Findings**

Effects of clearing treatment

Clearing of the parent stand of *A. saligna* by felling alone does not result in a significant reduction in soil-seed density after one year, although there is a gradual attrition of seeds over many years (assuming germinants are removed before attaining reproductive maturity) (1). By contrast, burning treatments generally reduce the seed bank by at least 90% in the first year after clearing (1), primarily through heat-induced mortality, but also through enhanced germination in surviving seeds (2). Percentage viability in *A. saligna* seed banks is high and is not affected by clearing method or time elapsed since clearing (2). Dormancy in *A. saligna* seed banks is also high, as seedling emergence accounts for only a very small proportion of the seed bank following felling of the parent stand (2, see also 9). However, following burning, a large proportion of the remaining viable seed bank emerges as seedlings (2). Exposure to dry heat breaks dormancy in a large proportion of *A. saligna* seeds at optimal temperature durations and a fast rate of germination ensues (4). *Acacia saligna* seeds survive high temperatures better than some indigenous legume species (4).

Seed banks of *A. cyclops* are significantly reduced by both felling and burning treatments one year after clearing (1,3). Following all treatments, seed bank decline is exponential, with most seed attrition occurring during the first year and little thereafter (1). In general, burning treatments reduce soil-seed density more than felling (1,3), but one treatment, "fell & burn", may be no more effective than felling alone (3). Percentage viability in *A. cyclops* seed banks is not always high (2) and to a large extent may reflect the varying percentage viabilities in seed crops produced in different localities or years (2,6), as the proportion of viable seeds remaining in the soil increases with time elapsed since removal of the parent

stand (2). Dormancy in *A. cyclops* seed banks is lower than in those of *A. saligna*, as a larger proportion of the seed bank emerges as seedlings in the former species (2, see also 9). In contrast to *A. saligna*, dormancy in *A. cyclops* is not broken by heat treatment (3,4) and germination may rather be enhanced by post-disturbance soil conditions (e.g. fluctuating temperatures) (4) or passage through the gut of birds (3).

Pre-dispersal seed predation

An indigenous alydid bug (*Zulubius acaciaphagus*) feeds on canopy-held seeds of *A. cyclops* in South Africa (5,6), but no equivalent insect has been observed to feed on seeds of *A. saligna* (pers. obs). *Zulubius acaciaphagus* occurs throughout the distributional range of *A. cyclops* in South Africa, but usually at fairly low densities (6). Feeding by *Z. acaciaphagus* significantly reduces seed viability (5,6) and promotes rotting (6). However, there is no evidence that such feeding increases spontaneous germination by breaking seed-coat imposed dormancy (6). Towards the north-western extreme of *A. cyclops*' distributional range, *Z. acaciaphagus* densities are high, resulting in the destruction of at least 84% of the annual seed crop (6). Therefore, in some localities net viable seed production and hence seed accumulation in the soil may be substantially reduced by this pre-dispersal seed predator (6).

Post-dispersal seed removal (7)

Seeds of both *Acacia* species placed in the litter layer are removed by indigenous ants (dispersers) and rodents (predators). In dense *Acacia* stands there is generally a surplus of seeds, but within a week, ants remove all *A. saligna* seeds presented to them compared to about 36% of *A. cyclops* seeds. Except at times of seasonal shortage, rodents are slow to remove seeds in dense stands. In stands of low *Acacia* density, seed removal by ants and rodents is both more rapid and complete than in dense stands, and at the lowest *Acacia* density investigated (10% PCC) the two

agents may compete for seeds. That rodents have the capacity to consume the entire *Acacia* seed crop in low density, satellite populations (see also 9), suggests that indigenous ants have played a critical role in burying and thus accumulating *Acacia* seeds in the soil. In dense *Acacia* stands, large seed banks may have accumulated both because of predator satiation and reduced predator density.

Seed burial and its effects

In sandy soils, *Acacia* seeds may be distributed to a depth of 300 mm or more, although the seed bank is usually concentrated in the upper 80 mm (10). Seed burial is facilitated by the actions of burrowing animals, particularly the larger rodents, but also occurs in the absence of obvious burrowing activity (10). In soil profiles disturbed by molerat (*Bathyergus suillus*) mound production, more seeds moved up than down the profile, some seeds being exhumed to the surface, compared to seeds in undisturbed profiles in which upward displacement was negligible (10). In addition, indigenous ants may actively bury *Acacia* seeds in nests below the soil surface (7). In areas in which burrowing agents are scarce (e.g. areas previously bare dunes) *Acacia* seed banks are concentrated more in the litter layer and upper soil profile (10).

Whereas surface seeds are exposed to predation and dispersal (7), buried seeds are lost primarily through germination and rotting (8,9), although shallow burial does not preclude rodent predation (9). Despite initially high levels of dormancy and viability, a large proportion of seeds buried 10-50 mm below the soil surface are lost in the first year through germination and rotting (8). Decay rate is not affected by seed density, and is much lower in *A. saligna* than in *A. cyclops* (8). Decay rates are significantly lower in the second than in the first year (8,9).

Seed longevity is much higher in *A. saligna* than in *A. cyclops*, but in both species it declines with depth of burial owing to enhanced rotting and/or germination (9). Seedlings of both species may emerge from depths up to 150 mm, but those of *A. cyclops* have greater potential to emerge from 150 mm than those of

A. saligna (9). Of seeds buried at 10, 50, 100 and 150 mm depths in the field, most *A. saligna* emergents were from 100 mm, whereas in *A. cyclops* most were from 50 mm depth.

(b) Discussion of original hypotheses

(i) *Seed bank size*

In South Africa, *A. saligna* and *A. cyclops* accumulate large seed banks in the soil (Table 1) as predicted for species subject to periodic disturbance (Thompson 1978). However, alien species accumulate large seed banks relative to indigenous species of comparable mediterranean-climate regions which are also subject to periodic disturbance (usually fires) (Table 1).

In nutrient-poor ecosystems, a high reproductive output may only be possible in species with specialised adaptations for nutrient accumulation. Thus in mediterranean Australia and South Africa, plants often have excess carbon to channel into leaves, the production of lignins and tannins, large inflorescences with copious nectar and sustaining fungal associates (Milewski 1983). In such ecosystems, acacias, with their associated symbionts, may be able to utilize a greater proportion of carbon for nutrient uptake, growth and reproduction relative to many non-legume species. However, in native habitats, a potentially high net reproductive output may be offset by parasitism and herbivory as well as by seed predation, and may be realized only when the species are released from those constraints. Therefore Thompson's (1978) hypothesis should be tested using seed bank data for *A. saligna* and *A. cyclops* in native Australian habitats. Thompson's (1978) hypothesis may be too simplistic as the seed bank is just one component of a species' life history syndrome and may be correlated with the other components. Hence coexisting species may have small or large seed banks owing to radically different life-history syndromes (*cf.* Keeley 1987).

Table 1. Soil-stored seed density (seeds.m^{-2}) for mature shrubs of mediterranean-climate regions with comparative data for alien *Acacia* species in South Africa

Indigenous species	Viable seeds.m^{-2}	Source
Acacia cyclops	0-94	Gill & Neser 1984
Acacia longifolia	6	Weiss & Milton 1984
Chrysanthemoides monilifera	46	"
Myrica cordifolia	6	Milton & Hall 1981
Ceonothus greggii	262	Keeley 1977
Ceonothus leucodermis	84	"
Arctostaphylos glauca	187	"
Arctostaphylos glandulosa	288	"
Alien Species		
Acacia cyclops	1 400-5 000	Holmes 1987 (1)
Acacia saligna	8 000-46 000	"
Acacia longifolia	2 000-3 000	Pieterse & Cairns 1986

(ii) *Types of seed bank*

Although seed bank size may be altered radically by translocating the species (see (i)), the "type" of seed bank should remain unaltered between native and translocated populations, although the persistent fraction may be overemphasized owing to greater inputs of non-predated seeds in the latter.

Acacia saligna produces a large crop (7) of predominantly hard seeds (9) which may remain dormant and viable in the soil for many years (2,8,9). Thus, as predicted, this species possesses a "Type IV" persistent seed bank (Thompson & Grime 1979) and as dormancy is readily broken by heat treatment (4) and fire (2), its seed bank can also be considered "disturbance-coupled" (Grubb 1988).

By contrast, *A. cyclops* does not have a "Type IV" persistent seed bank (Thompson & Grime 1979) as a large proportion of the annual seed crop germinates or rots in the first year (8,9). However, a very small proportion of seeds may remain dormant in the soil, thus its seed banks cannot be considered transient (*sensu* Thompson & Grime *ibid.*). There is no evidence from this study that *A. cyclops* seed banks are "disturbance-coupled" (Grubb 1988). Dormancy is not broken by heat treatment (4) and seedling emergence is not enhanced following burning treatments (3). Furthermore, some seedlings emerge under dense stands

(3), therefore removal of the vegetation cover (as in erosion-related disturbance) is not an essential prerequisite for germination. The seed bank of *A. cyclops* most closely conforms to the "Type III" persistent seed bank described by Thompson & Grime (1979) and may be "disturbance-uncoupled" (Grubb 1988). If this is true, then *A. cyclops* is an opportunistic species, which relies on dispersal into recently disturbed areas for successful establishment. However, by maintaining a small dormant seed bank *A. cyclops* may also reduce the risk of local extinction.

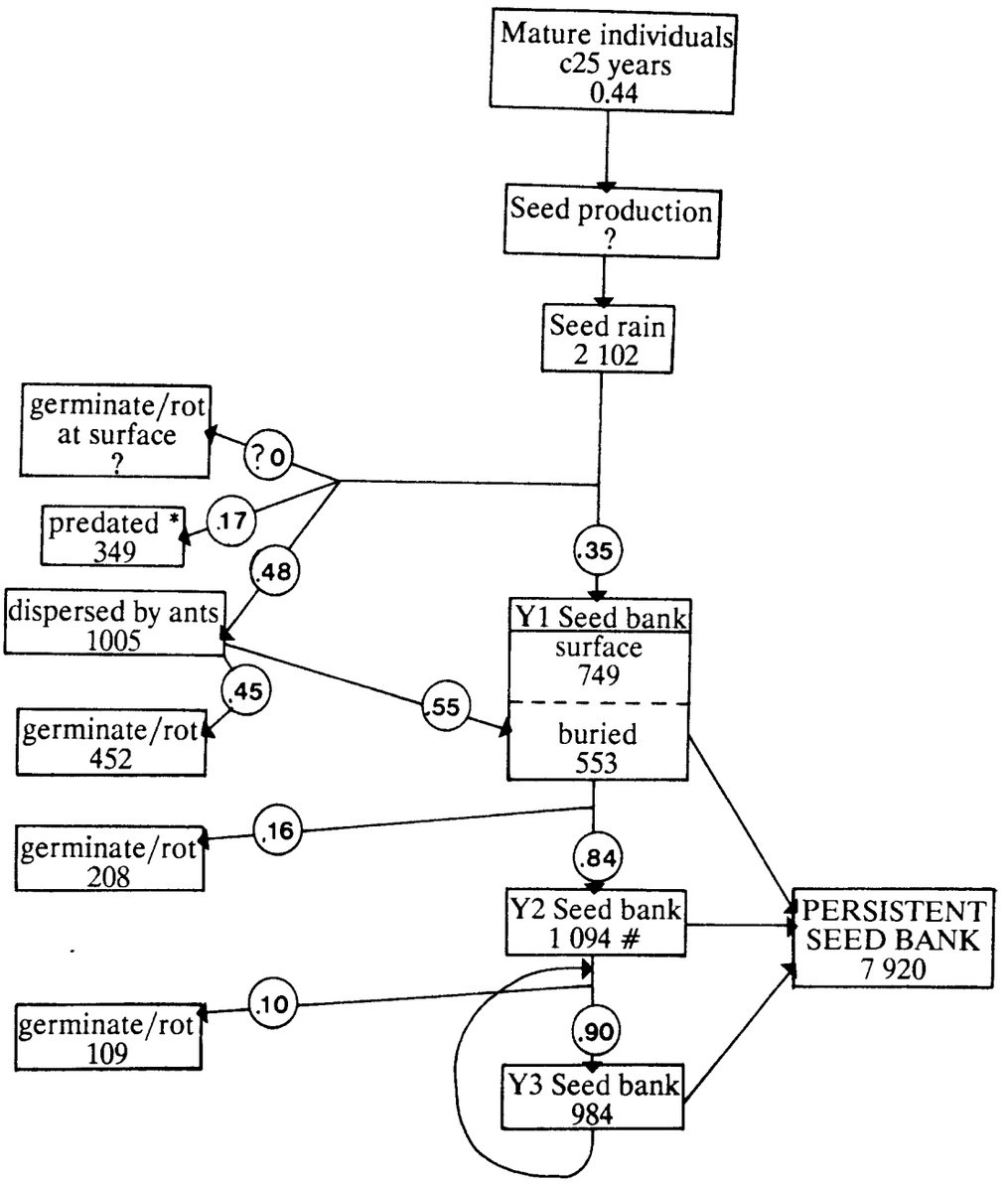
(iii) *Seed bank decay*

Decay rates in populations of alien *Acacia* seeds in the soil do not support the constant and continuous death risk model, which was developed from data on annual weed seeds in the soil (Roberts 1972). In *Acacia*, probability of death decreases with increasing time in the soil (8,9) (Deevey Type III decline), as the "soft" or non-dormant fraction is lost first (both through germination and rotting) and the persisting fraction consists of predominantly "hard" seeds which have a greater probability of survival than the original population (8). In annual weeds, depletion of seed populations is largely due to the loss of dormancy resulting in germination, with probability of germination being constant from one year to the next (Roberts 1972). The assumption upon which the seed depletion model rests, is that the probability of losing dormancy remains constant over time. Although the assumption may hold true for some annual species with persistent seed banks, it is unlikely to apply to a wider range of species, either if longevity is under phenotypic control, or if seed depletion depends more upon environmental factors, such as pathogens and predators, than characteristics of the seed (Lonsdale 1988). Therefore the use of seed survivorship models may be of limited value and, as more data are gathered, it may be found that, as for seedlings and plants, variability in survivorship curves is the rule rather than the exception (Lonsdale 1988).

(iv) & (v) *Seed bank processes*

That the seed fraction is the critical part of the life-cycle in both alien *Acacia* species is exemplified by the high density of seeds in soil beneath dense stands (1,3) and the high density of seedlings emerging following disturbances (2,3). Contrary to prediction, however, different seed bank processes provide the key to invasive success in the two species.

Life-tables (Figures 2-4) summarize major seed bank processes.



* Partitioning of seeds between predators and dispersers was calculated using cumulative proportions removed in bimonthly trials (7).
\# assumes no seeds remain on surface after one year

Figure 2. Life-table for dense *A. saligna* (numbers are per m^2). Data are combined from Silvermine (1,7) and Pella (8)

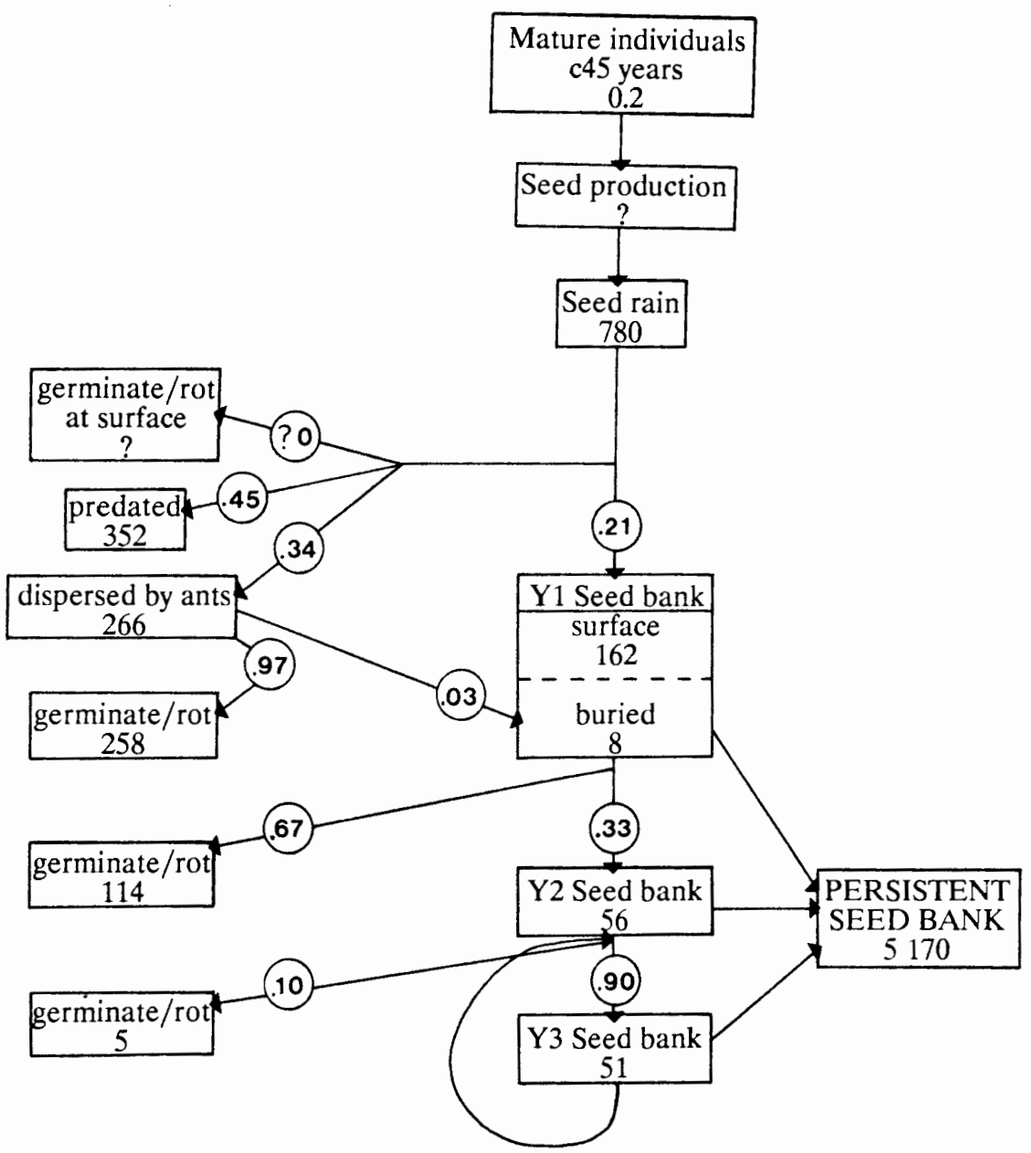


Figure 3. Life-table for dense *A. cyclops*. Data are combined from Cape Point (7) and Pella (8) (numbers are per m^2)

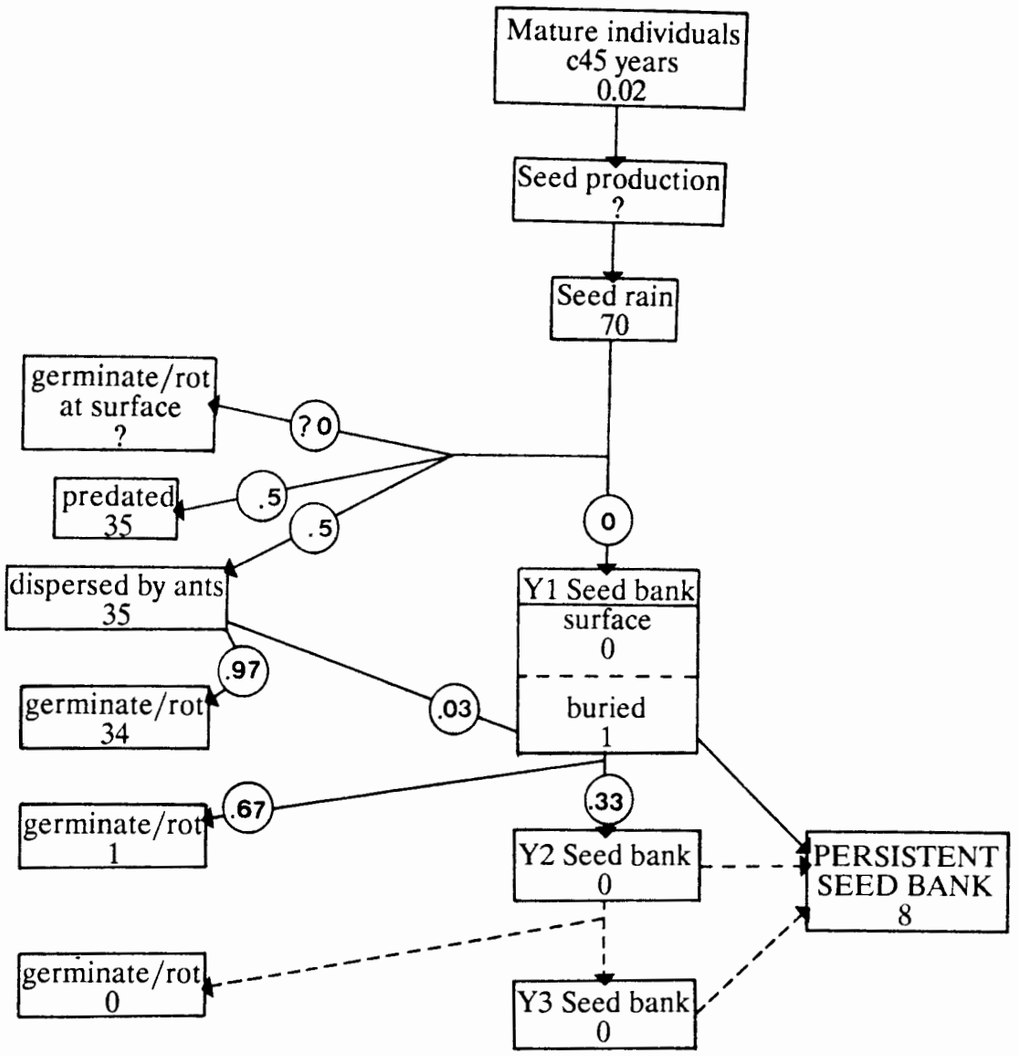


Figure 4. Life-table for low density *A. cyclops* (10% PCC). Data are combined from Cape Point (7) and Pella (8) (numbers are per m^2)

In mature *A. saligna* stands, seed production is high and a large proportion of the seed crop survives the first year to enter the seed bank in the soil (Figure 2). A large proportion of these seeds remain dormant and viable, resulting in a rapid accumulation of seeds. High longevity in *A. saligna* seeds, coupled with a rapid germination response following fire (see (ii) above) are therefore key processes in the species' seed bank dynamics leading to invasive success.

By contrast, in mature, dense *A. cyclops* stands, accumulation of seeds in the soil is very slow, primarily owing to low seed longevity (Figure 3). In low density stands, seed accumulation is negligible (Figure 4). The large seed banks which have been measured under this species are difficult to explain in terms of data collected on seed bank processes during this study. However, seed banks are often the result of dynamic fluctuations in inputs and outputs from year to year rather than a steady accumulation of seeds (Thompson & Grime 1979, Keeley 1987, Lonsdale *et al.* 1988), thus certain seed cohorts may be more resistant to decay or less exposed to predation than others and thus contribute more seeds to the persistent bank. Alternatively, it may be argued that in areas where *A. cyclops* was planted to stabilize bare dunes, seed predators and burial agents were scarce (10), thus promoting a more rapid accumulation of seeds in the soil. Subsequently, seed predators may have colonised these *Acacia* thickets and slowed down the rate of seed accumulation. It is also possible that a pre-dispersal seed predator may have only recently colonised *A. cyclops*, further reducing seed accumulation in recent years (5,6). Unlike *A. saligna*, *A. cyclops* is not adapted to fire (see (4)). The large seed banks which have accumulated under *A. cyclops* stands in the past, ensure its persistence in those areas, but the other key process (not measured in this study) would seem to be dispersal by birds (Middlemiss 1963, Winterbottom 1970, Glyphis *et al.* 1981, Prys-Jones & Fraser 1987, Hofmeyr 1989), as this maintains invasion pressure on neighbouring uninfested areas.

Despite being closely related species with putatively long-lived seed banks in the soil, it cannot be assumed that the same processes lead to invasive success in

A. saligna and *A. cyclops*. *Acacia saligna* produces a vast surplus of seeds annually and has the potential for exponential expansion. Although it has no natural means of long-distance dispersal, an artificially assembled system between *A. saligna* and birds has developed in South Africa (Knight 1988), allowing it to invade new areas. *Acacia cyclops* does not produce such a vast surplus of seeds, even in dense thickets, and although the rate of seed removal by birds has not been measured, it would appear that avian dispersal has contributed to its currently wide distribution.

Testing of Assumptions within the theoretical framework

(i) *Acacia saligna* seeds in the soil have high percentage viability and dormancy as predicted, whereas those of *A. cyclops* have a wide range in percentage viability and dormancy (2).

(ii) As expected, seeds have the potential to persist for many years in the soil: a minimum of eight years in *A. saligna* and 12 years in *A. cyclops* (1). However, the probability of survival is much higher in *A. saligna* than in *A. cyclops*: respective half-lives for fresh cohorts of seeds are 1.2 years and 0.2 years (8).

(iii) The absence of any obvious pre-dispersal seed predator on *A. saligna* in South Africa may contribute to its high percentage viability, as a seed-feeding alydid bug reduces percentage viability in *A. cyclops* seeds (5,6). However, there is no evidence that viability is maintained whilst dormancy is broken by such predation (6).

(iv) Low levels of pre-dispersal seed predation (6) have contributed to the production of large crops of viable seeds, which have the potential to form large seed banks. In dense stands, low levels of granivory have also contributed to the formation of large seed banks (7). However, in low density stands, granivores (notably small mammals) can potentially consume the entire seed crop and were it not for the actions of indigenous ants, which rapidly move seeds below ground to their nests, seed accumulation in such areas would probably be negligible (7).

(v) Seeds of *A. saligna* germinate readily following heat treatment, whereas, contrary to prediction, those of *A. cyclops* show no positive response (4).

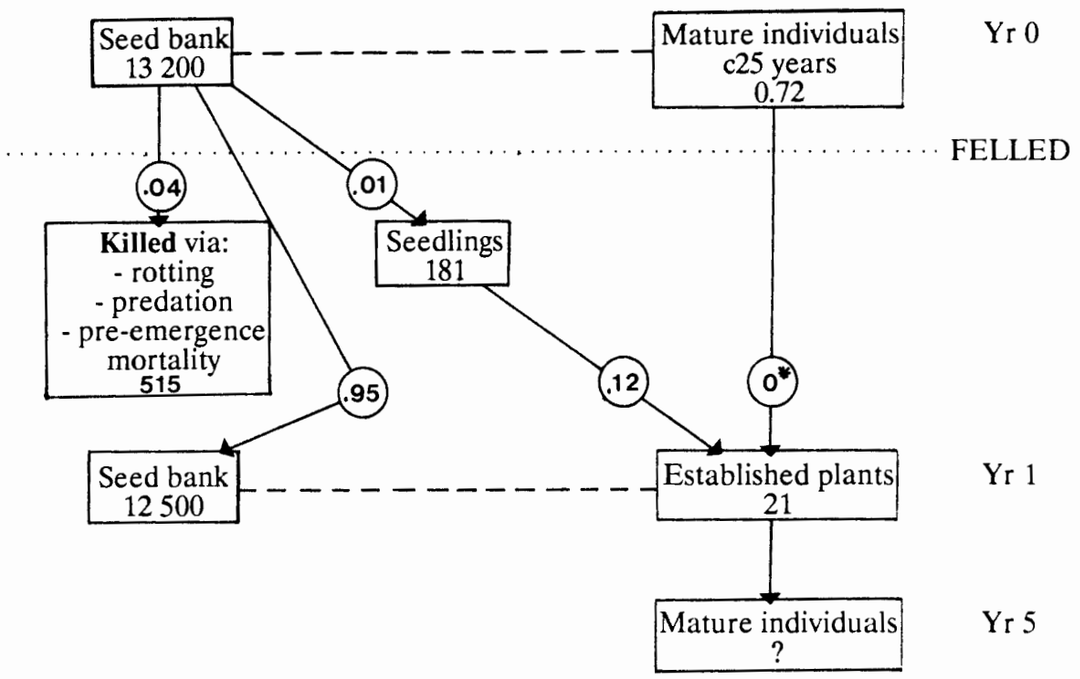
(vi) Burning methods result in significant seed bank reductions in both species and are superior to non-burning methods in *A. saligna* (1). However, in *A. cyclops*, felling alone results in a significant decrease in seed banks (1,3) and burning methods may be superior only in sites where seed banks are concentrated near to the soil surface (3).

(c) **Implications for control**

Some general recommendations for the control of alien *A. saligna* and *A. cyclops* can be made from a study of their seed bank dynamics (see Figures 5-8). Unfortunately however, it is not possible to predict maximum seed longevity in the soil as the rate of decay follows a "Deevey Type III" curve (8). Longevity in even the lowest density seed population remaining after the most effective clearing treatment may be extremely high, which emphasizes both the near-impossibility of total eradication of these species from the natural vegetation and the importance of continuous follow-up control in their clearing programmes.

Dense stands

In *A. saligna*, the large seed banks which accumulate beneath dense stands (1), together with the high level of seed-coat imposed dormancy in the absence of heat treatment (2,4), should be the focus for control measures. Thus, methods which include burning are essential for a significant reduction in the seed bank.



* Probability of resprouting in single-stemmed individuals >30 mm diameter cut at the base is nil (Macdonald unpublished data)

Figure 5. Life-table for dense *A. saligna* following felling and clearing. Data are from Cape Point (1,2)

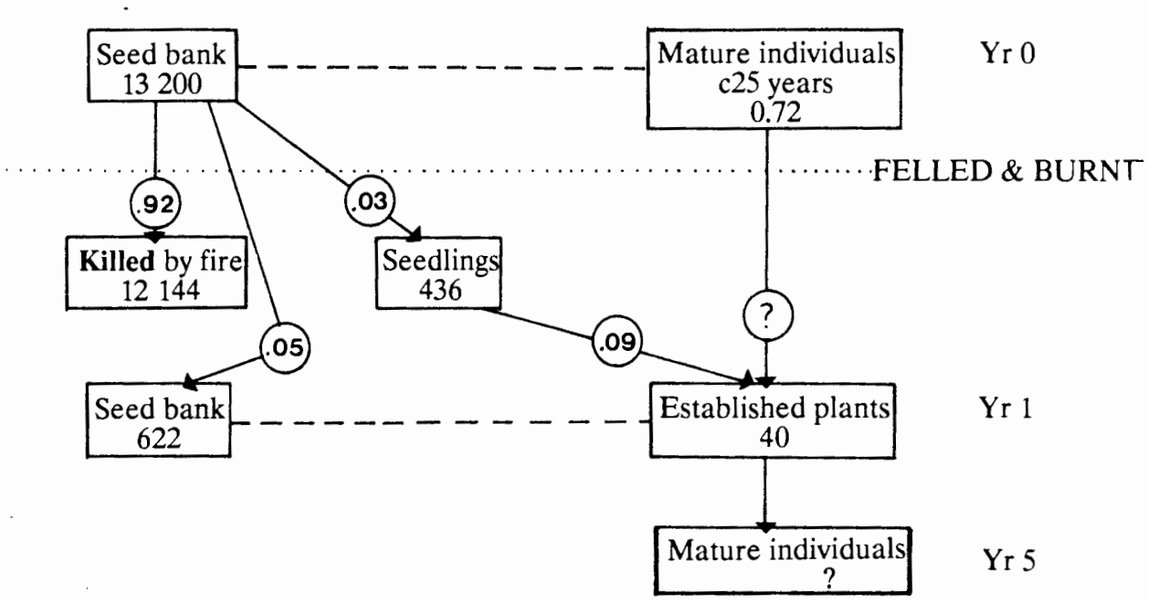


Figure 6. Life-table for dense *A. saligna*, felled and burnt. Data are from Cape Point (1,2) (numbers are per m^2)

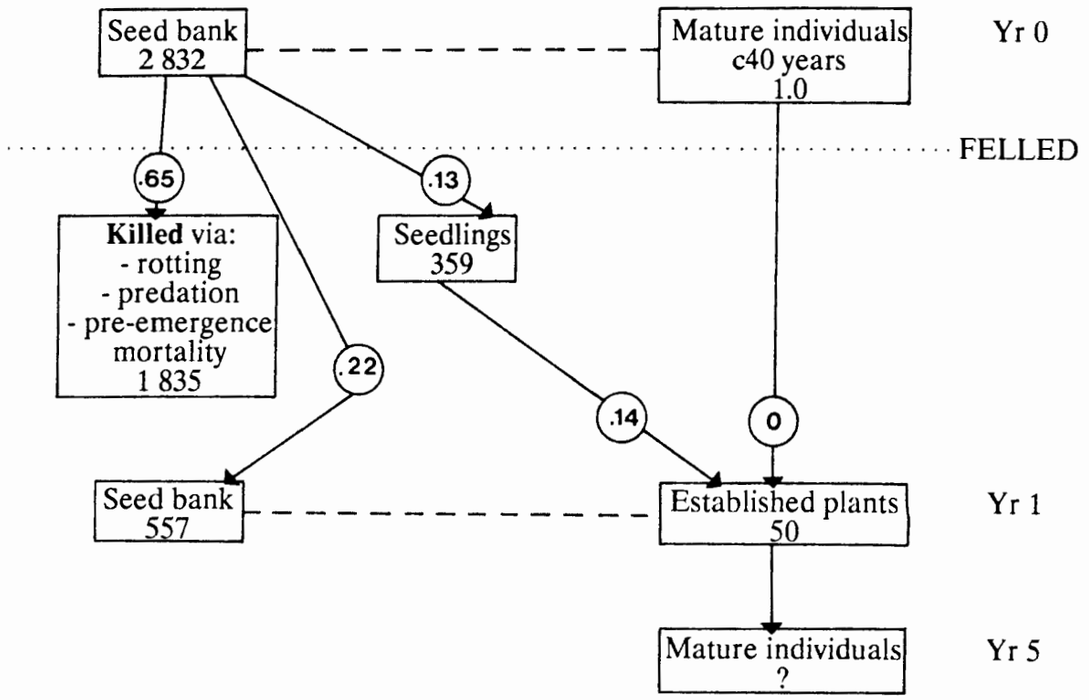


Figure 7. Life-table for dense *A. cyclops*, felled and cleared. Data are from Walker Bay (3)

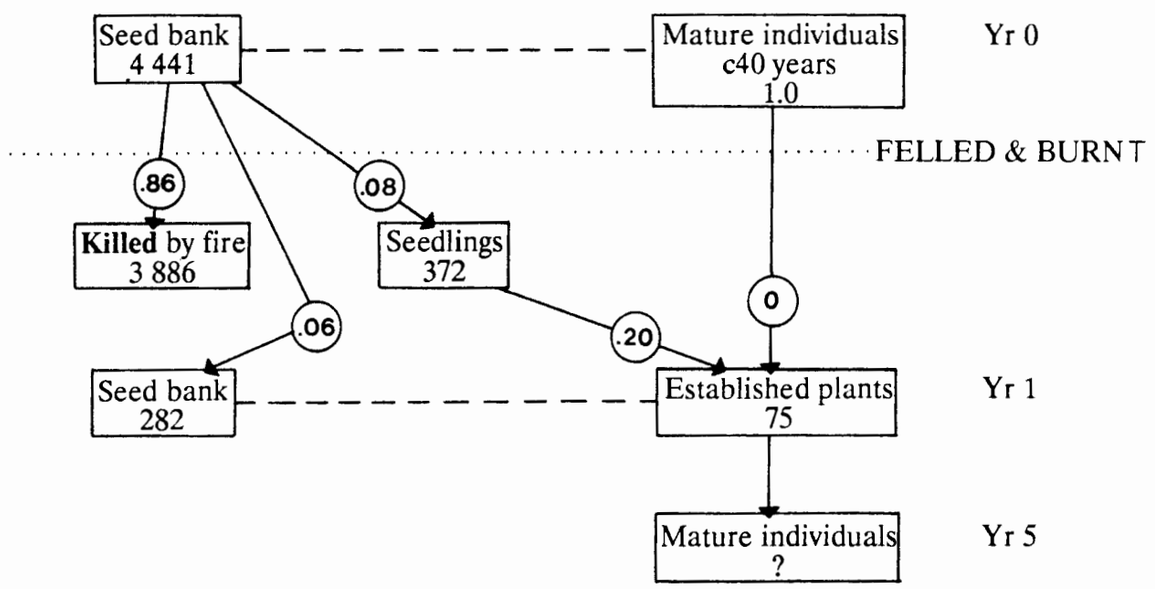


Figure 8. Life-table for dense *A. cyclops*, felled and burnt. Data are from Walker Bay (3) (numbers are per m^2)

In *A. cyclops*, the advantage of burning methods over felling alone is less significant, owing to a low probability of seed survival in the soil (8,9). Together with a lack of germination response following heat treatment (3,4), this suggests that the choice of clearing treatment should rest on the size and depth distribution of the seed bank and the type of habitat invaded. If seed banks are large and concentrated towards the soil surface as may be the case in bare-dune areas planted with *A. cyclops*, burning may be the more effective treatment, especially if labour is scarce and a "burn-standing" treatment can be safely applied. By contrast, in fynbos communities invaded by *A. cyclops*, the seed bank is likely to be less concentrated at the soil surface (10) and burning would kill a smaller proportion of the seed bank. Furthermore, as fires may be very intense in dense *Acacia* stands, presumably owing to the high biomass (Appendix I), any indigenous propagules persisting in the area may be killed.

In dense monospecific stands of either species, high intensity fires should be aimed for, as these will kill a larger proportion of the seed bank than low intensity fires. Provided that a high intensity fire can be achieved in late spring or early summer, this season should be opted for so that the post-fire germination flush (particularly in *A. saligna*) is exposed to maximum drought stress (2,3). In areas which have already been highly disturbed by man's activities, it may be feasible to mechanically invert the soil profile following the clearing treatment and prior to a revegetation programme, so that longevity in persisting *Acacia* seed populations is greatly reduced (9).

Light infestations and "satellite" populations

Small, outlying (satellite) populations and fynbos communities sustaining light infestations should be primary targets for control, as these areas may act as centres for further spread of the invaders (Mack 1985, Moody & Mack 1988) and may eventually contribute more to their spread than the original dense stands (Moody & Mack 1988). Although granivores can potentially destroy the entire seed crop in

low density *Acacia* populations (7), dispersal by indigenous birds (long-distance) (Middlemiss 1963, Winterbottom 1970, Glyphis *et al.* 1981, Prys-Jones & Fraser 1987, Knight 1988, Hofmeyr 1989) and ants (short-distance) (7) gives the potential both for range expansion and growth of the satellite populations, especially in *A. saligna* which has a much higher probability of seed survival than *A. cyclops* (9).

In satellite populations it is essential to curb seed production and hence further dispersal. Felling kills *A. cyclops* and is apparently also effective for *A. saligna* provided that the plant has not already coppiced (IAW Macdonald unpublished data). If the plants have already set seed, seed banks under isolated *A. cyclops* should be negligible, whereas under *A. saligna* they may be considerable. Thus in *A. saligna*, follow-up control is particularly important, especially after the area has burnt.

(d) **Priorities for future research**

A major gap in this study of alien *A. saligna* and *A. cyclops* seed population dynamics in South Africa is the rate of seed removal by avian dispersers. Long-distance dispersal is essential to the spread of any species, and if mutualistic relationships are established between alien plants and local dispersers, the aliens could spread exponentially. If avian dispersal is an important component of *Acacia* population dynamics, then the introduction of appropriate seed-attacking agents may be the only feasible method of control in the long-term. If avian dispersal is relatively unimportant, however, a continuous programme of manual clearing should eventually control the invaders.

The colonization of *A. cyclops* by *Zulubius acaciaphagus* (5,6) in South Africa merits further study. Little is known of the insect's population dynamics, whether it is expanding its range as a result of *A. cyclops* encroachment and whether it could be used as a biological control agent against *A. cyclops*.

The potential importance of indigenous ants in removing *Acacia* seeds to "safe sites" was highlighted in this study (8) and merits further attention. In

particular, the efficiency of ants in moving seeds below ground in different fynbos communities and at different *Acacia* densities, and the depth to which seeds are buried, should be investigated.

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APPENDIX I

FIRE BEHAVIOUR AND SOIL TEMPERATURES DURING FIRE IN ACACIA CYCLOPS AT WALKER BAY STATE FOREST

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1. INTRODUCTION

The seed biology and dynamics of the seed bank in Acacia cyclops A. Cunn. ex G.Don, an alien invasive plant in the southwestern Cape, are being studied as part of a project funded by the CSIR. This species builds up large reserves of hard-coated seeds in the soil. These reserves are a constant problem where attempts are made to control this species. The effects of fire on the seed bank need to be quantified in order to assess the efficiency of fire as a control measure. A site on the Walker Bay State Forest was burnt as part of the management of the area, and the opportunity was used to assess the effects of fire on the seed bank. The purpose of this report is to document the fire behaviour and soil temperatures during the fire. It is intended to serve as a reference when interpreting the results of the study.

2. THE STUDY SITE

Walker Bay State Forest (32°25'S, 19°24'E) lies to the east of the town of Hermanus on the southern Cape coast. The area consists of low dunes with a maximum elevation of 50m above sea level. Soils are unstructured deep sands derived from shelly aeolian deposits. The vegetation of the area is predominantly south coast strandveld (Moll et al 1984) with fynbos elements becoming more prevalent inland. Prior to 1940 much of the area comprised unvegetated mobile dunes. This area was stabilised using Acacia cyclops (approximately 38 years age at this study site). In January 1982 an accidental fire, which started on a property to the east of the reserve, spread into the area and burnt out 425 ha of A. cyclops. This fire missed a few pockets of A. cyclops, including the present study site. Good recovery of indigenous vegetation followed and this was encouraged by weeding out regenerating acacias. However, on the inland dunes (which probably coincide with the previously mobile dunes) percentages canopy cover is still low.

3. METHODS

3.1 Experimental design

Three adjacent stands of Acacia cyclops were burnt following different treatments. The treatments were: (i) plants left standing live; (ii)

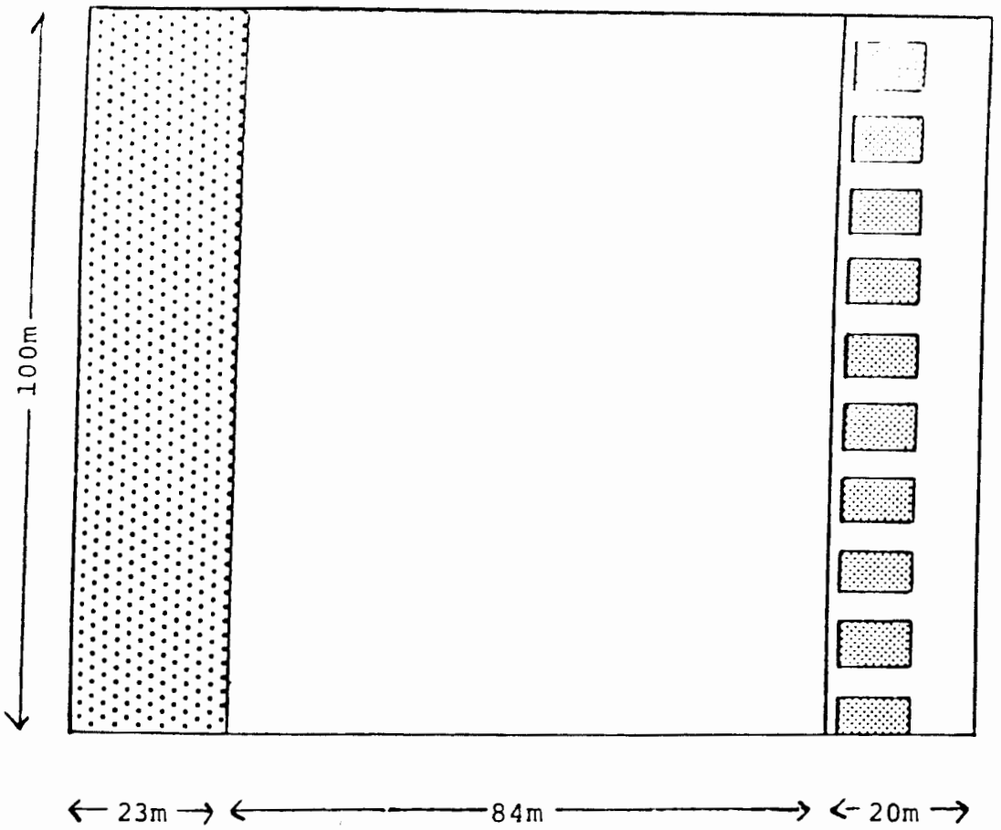

Figure 1: Layout of three treatments in Acacia cyclops at Walker Bay. The left (shaded) area is where A. cyclops were slashed and allowed to dry where they fell. In the centre (unshaded) area, A. cyclops was burnt standing. On the right, A. cyclops was felled and piled as indicated by the shaded blocks.

plants slashed; and (iii) plants slashed and piled. The layout of the plots is shown in Figure 1.

3.2 Pre-fire biomass

The diameter at 10 cm above the ground of all trees occurring on three plots (5 x 5 m) was measured. The biomass of Acacia cyclops on the site was estimated by entering diameters in the equations given by Milton and Siegfried (1981). Litter depth was measured at 10 random points, and the data were used to estimate litter mass using the BEHAVE system (Burgan and Rothermel 1984). The BEHAVE system provides an estimate by means of using established relationships between litter depth and mass.

3.3 Conditions during the fire

Weather during the fire was recorded at one minute intervals. Temperature and relative humidity were estimated with an Assman asperated psychrometer. Windrun was recorded with a cup anemometer. Wind gusts were recorded with a handheld cup anemometer.

Rate of fire spread was determined by timing the progress of the fire from one end of the plot to the other (a known length). Flame lengths were estimated visually during the fire and checked on photographs taken during the fire. The amount of fuel consumed was estimated by visually assessing the percentage of various components of the biomass consumed by the fire. Fireline intensity was estimated by two different methods. It was calculated using Byram's formula $I = Hwr$ where I is the intensity in kW m^{-1}, H is the heat yield (18 500 J g^{-1} was used, Trollope 1984) w is the mass of fuel consumed and r is the rate of fire spread. The heat of combustion values given by Trollope were reduced for moisture content to estimate heat yield (Byram 1973). Secondly, fire intensity was estimated from flame length (van Wilgen 1986).

Maximum soil temperatures were recorded using "thermindex" cards at 10 points and two depths in each of the three treatments. Thermindex cards will indicate whether a given temperature was exceeded, and are available for a range of temperatures. Published accounts of soil temperatures

during fires under fuel piles indicated that temperatures in the range of 76° to 280°, and 68° to 100°C could be expected at 25 and 51 mm depth respectively (Beadle 1940, Humphhreys and Lambert 1965, Floyd 1966). At each point the cards, mounted on an aluminium plate, were buried at 10 and 40 mm. The cards at 10 mm would indicate temperatures in the range 121 to 260 °C, while those at 40 mm were for the range 121 to 204 °C. Soil temperatures under live vegetation fires have been shown to rise little (Beadle 1940, Martin 1966, van Wilgen and Forsyth 1983) so under the "standing live" treatment and the "felled" treatment (which had a lower fuel load then the piles) the cards were chosen to indicate temperatures in the range 40,6 to 160°C and 40,6 to 71°C at 10 mm and 40 mm respectively. At five of the points an extra card for the range 121-160 °C was buried at 10 mm depth.

Fire danger indices were calculated using a fynbos fuel model (van Wilgen 1984) and weather data from Prinskraal (34°38´S, 20°07´E). The weather data for 50 days prior to the fire were used in the manner described by Van Wilgen and Burgan (1984) in a fire danger rating system. The purpose of this calculation was to record the indices prevalent on the day of the fire as they will be a useful reference for future burning operations where the fire danger rating system is in use.

4. RESULTS

4.1 Conditions during the fire

The fire took place on 16 January 1986. The pre-fire biomass and other conditions prevalent during the fire are given in Table 1. The conditions during the fire were relatively windy for prescribed burning. The energy release component at Prinskraal was 12, which is two points below average for January. The energy release component has been found to be a reliable indicator of potentially severe fire conditions (van Wilgen 1985; G. Ruddock, pers. comm.), and energy release components exceeding about 18 indicate dangerous conditions. Seen in this light, the conditions were moderate. Fire behaviour and related parameters are given in Table 2. Flame lengths were particularly high in the standing thicket, and fireline intensities were correspondingly high. Both the intensities and

the flame lengths exceeded those recorded under relatively severe conditions in fynbos (van Wilgen et al 1985). Fireline intensity was not calculated for the piles as the measure is not valid for such conditions, where residual burning continues for a long period after the passage of the main flaming front.

4.2 Soil temperatures

Temperatures in the soil exceeded the expected values. Under the piles all of the temperatures exceeded the maximum values allowed for (260°C and 204°C at 10 mm and 40 mm respectively) in all 10 replicates. In the felled treatment at 10 mm depth, all five cards with a temperature ceiling of 116°C and three out of four cards with a ceiling of 160°C exceeded those values. The ninth card recorded 71°C and the tenth was unrecovered. At 40 mm depth, eight out of nine cards, exceeded the ceiling temperature of 71°C and the remainder recorded 49°C.

In the standing live treatment again only nine replicates were recovered. At 10 mm depth, all four cards with a ceiling temperature of 116°C and four out of five cards with a ceiling of 160°C exceeded those values. The remainder recorded 116°C. At 40 mm depth, eight out of nine cards exceeded the ceiling temperature of 71°C and the remainder recorded 46°C.

5. DISCUSSION

Research into the effects of fire on the soil-stored seed banks of Acacia cyclops (and other seed banks) is a fairly new field. The aim of the research is to quantify the effects of fire on seed viability and germination. In order to give these quantifications predictive value, it is necessary to have an accurate description of the fire that caused the effects observed. If this is done, the type of fire that will achieve the desired result can be specified, thus allowing managers to burn to achieve certain aims.

In this fire, the temperatures that prevailed in the soil were unexpectedly high, and we are therefore unable to quantify this aspect accurately. However, it would be useful to determine the maximum temperatures to

which A. cyclops seeds are resistant, so that we could determine whether the temperatures exceeded are sufficient to kill the seeds.

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Table 1. Conditions of weather and fuel on the site of a fire in *Acacia cyclops* on 16 January 1986 at Walker Bay State Forest.

Mean air temperature (°C)		26.4
Mean relative humidity (%)		38.6
Mean windspeed (m s^{-1})		2.96
Wind gusts (max.) (m s^{-1})		12.0
Fuel moisture contents (% of dry mass)		
Live foliage		120.4 (range 111 - 139)
Dead Twigs and leaves		12.1 (range 11 - 13.2)
Dead sticks > 6 mm		13.1 (range 12 - 13.9)
Pre-fire biomass (g m^{-2})		
Foliage	1250	
Twigs	3387	
Wood	3389	
Litter	1017	
Total	9043	
Fuel depth (height of trees, m)		4

Fire danger indices (fynbos fuel model, weather data from Prinskraal) The figure in parentheses is the mean for January at Prinskraal.

Ignition component	12	(22)
Spread component	35	(110)
Energy release component	11	(13)
Burning index	46	(80)

Table 2. Fire behaviour and related parameters at a fire in Acacia cyclops on 16 January 1986 at Walker Bay State Forest.

Parameter	Under piles	Standing thicket	Felled thicket
Biomass consumed (g m^{-2})	8590+	7687*	8590+
Rate of spread (m s^{-1})	0.01	0.2 - 0.6	0.06
Flame length (m)	5	8 - 15	4
Fire intensity (kW m^{-1})			
From flame length	not valid	24 881 - 97 337	5 529
From Byram's formula	not valid	20 272 - 60 816	9 534
Maximum soil temperatures (°C)			
At 10 mm below surface	>260	116 - >160	71 - >160
At 40 mm below surface	>204	46 - >71	49 - >71

+ 95 % of total mass
* 60 % of woody mass and 100 % of all other components.